Definite strobili were present, in *Lepidodendron*, at the ends of the branches, in *Sigillaria*, in whorls along the stem. The sporophylls and foliage leaves were rather similar in form. As in all lycopods, the large sporangia were solitary, adaxial, and unilocular. The ligule was situated beyond the sporangium. The Lepidodendrales were heterosporous, the megasporangia generally containing 8 to 16 megaspores. In some cases trabeculae, consisting of sterile plates forming incomplete partitions, were present both in the microsporangia and megasporangia.

The gametophytes were developed inside the spores. The nature of the sperms is unknown. The archegonia were similar to those of *Selaginella*. The embryo is also unknown. In *Lepidocarpon*, a cone genus, the mature megasporangium had only one megaspore and, except for a narrow opening at the top, was invested by an integument that arose from below. This sporangium, although seed-like, was shed with the sporophyll before fertilization took place.

4. Isoetales

Isoetes is the only living genus belonging to the Isoetales. It has about 60 species widely distributed throughout temperate regions but rare in the tropics. It grows on muddy flats, in wet meadows, along stream and pond margins, or submerged in shallow water. A few species grow in drier habitats. Fossils resembling *Isoetes* are known from the Cretaceous and Tertiary periods.

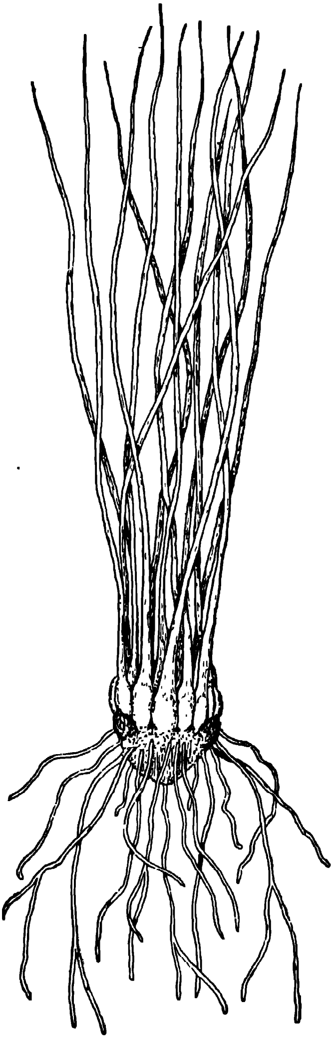

FIG. 198. *Isoetes nuttallii*, natural size.

Sporophyte. Superficially *Isoetes* is entirely different in appearance from any other living pteridophyte, resembling a small rush or tufted grass. Its common name is "quillwort." The stem is erect, tuberous, unbranched, and very short (Fig. 198). It gives rise to a crowded rosette of linear, spirally arranged leaves that are commonly about 5 to 15 cm., rarely 30 cm. or more, in length. The stem is either two-lobed or three-lobed, depending on the species. It is covered by overlapping leaf bases. Between its lobes arise numerous dichotomously branched roots. As in *Selaginella,* each leaf has a ligule, arising at its base on the adaxial side. The root and stem grow by means of a meristem (Fig. 199). The stem has both an apical and a basal meristem.

Vascular Anatomy. Each leaf has a single vascular bundle and four long air passages with numerous transverse partitions. Stomata are present only on leaves exposed to the air. The stem structure is rather complicated and difficult to interpret. Many botanists regard the upper part of the stem, which bears the leaves, as the stem proper and the lower portion, which bears the roots, as a rhizophore, although no such differentiation is evident externally.

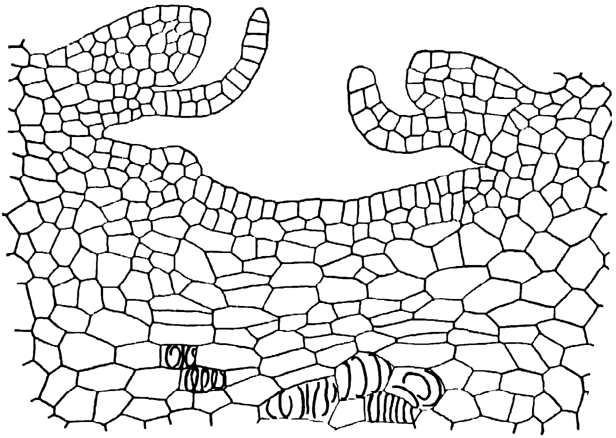

FIG. 199. Longitudinal section through the stem tip of *Isoetes howellii,* showing the apical meristem and developing sporophylls, each with a prominent ligule, ×300

The vascular cylinder, representing a greatly reduced protostele, is surrounded by an extensive cortex (Fig. 200). A notable feature of the stem of *Isoetes* is the occurrence of secondary thickening. The primary xylem, consisting of extremely short tracheids intermixed with considerable parenchyma, is surrounded by a narrow zone of primary phloem. This, in turn, is enclosed by a "prismatic layer," which represents the internal product of cambial activity. On the outside the cambium adds new tissue to the cortex. This tissue, which is parenchymatous, has the position of secondary phloem but not its structure. The tissues forming the prismatic layer are not uniform, but are differentiated into alternating zones of thin-walled and thick-walled cells. The thin-walled cells are ordinary parenchyma, while the thick-walled cells are lignified and have scalariform and reticulate markings. Thus the prismatic layer has the position of secondary xylem but not its typical structure. Whether the prismatic layer contains any secondary phloem, as has been claimed, is a matter of considerable uncertainty.

As cambial activity continues, the outer tissues of the stem are constantly sloughed off, the cortex finally being made up wholly of secondary tissue. Numerous leaf traces arise from the stele of the stem, one going to each leaf. In the lower part of the stem (rhizophore) root traces similarly pass from the stele to the roots. The root traces contain much more xylem and phloem than the leaf traces.

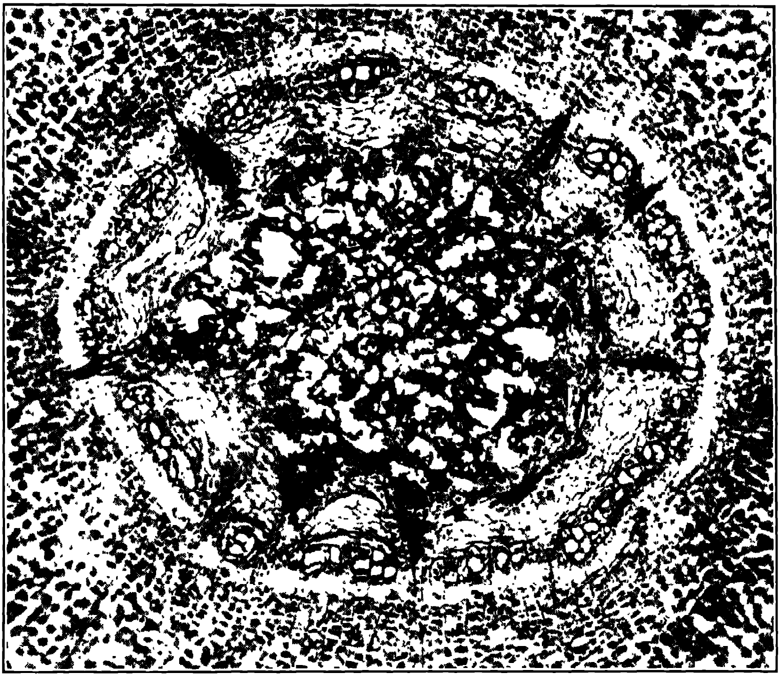

FIG. 200. Cross section of the central portion of the stem of *Isoetes howellii*, × 100 The primary xylem, in the center, is surrounded by a narrow zone of primary phloem enclosed by tissues derived from the cambium.

Sporangia. *Isoetes*, like *Selaginella*, is heterosporous, but nearly all the leaves are sporophylls. As a rule, the outer leaves bear megasporangia and the inner ones microsporangia, while the few central leaves are sterile. The sporangia, mostly 4 to 7 mm., but up to 10 mm. in length, are larger than those of any other living pteridophyte. They are solitary and adaxial, each one being sunken in a cavity at the base of the sporophyll just below the ligule (Fig. 201*A*, *B*). Each sporangium is partially or completely overgrown by a membrane called the *velum*. The microsporangia may produce as many as 300,000 microspores, the megasporangia up to 300 megaspores. In each of the two kinds of sporangia sterile plates, called *trabeculae,* extend inward to form incomplete partitions. The spores are freed by the gradual decay of the sporangium wall.

The sporangium arises from a transverse row of initials, three or four in number, and is eusporangiate in development (Fig. 201*C*). In early stages the two kinds of sporangia are indistinguishable from each other.

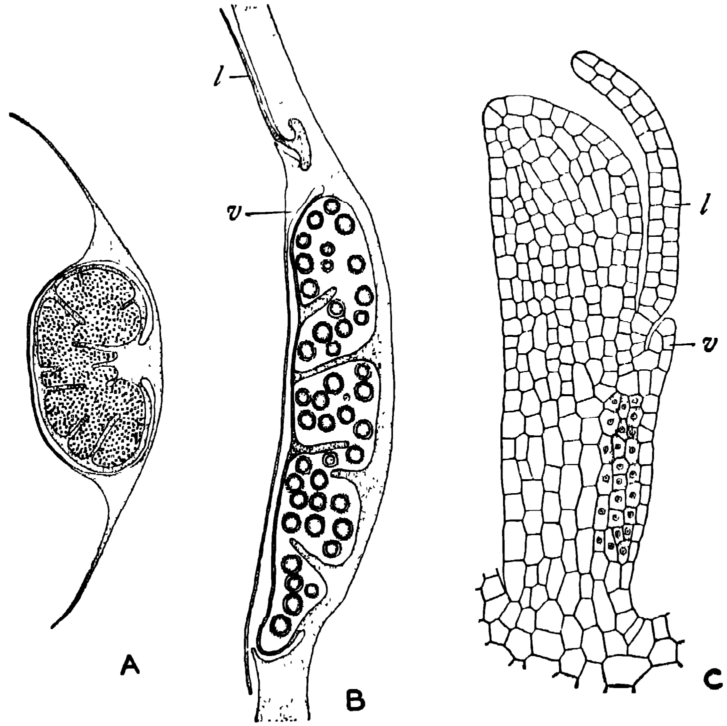

Fig. 201. Sporangia of *Isoetes.* *A*, cross section of microsporangium of *Isoetes nuttallii,* ×15; *B*, longitudinal section of megasporangium of *Isoetes nuttallii,* ×10; *C*, longitudinal section of young microsporophyll of *Isoetes howellii,* showing sporogenous tissue (shaded), ×250; *l*, ligule; *v*, velum.

After a large amount of potentially sporogenous tissue has been differentiated, some of it forms the sterile trabeculae. The sporangium wall consists of four layers of cells, the inner layer forming a tapetum that also borders the trabeculae (Fig. 202). The tapetum does not disorganize for a long while. In the microsporangium all the cells not taking part in the formation of the wall, trabeculae, and tapetum become functional spore mother cells. In the megasporangium the trabeculae are fewer and thicker, the tapetum comprises several layers, and most of the spore mother cells divide and contribute nourishment to a much smaller number that enlarge and form tetrads. As in *Selaginella,* the megaspore wall is very thick.

Gametophytes. The male gametophyte, like that of *Selaginella*, is developed inside the microspore and similarly consists of a small prothallial cell and an antheridium (Fig. 203). The latter has a sterile jacket of four cells investing four spermatogenous cells, each of which gives rise to a single sperm. It is noteworthy that only four sperms are produced, as this is the lowest number in pteridophytes. The sperms are large, coiled, and multiciliate, thus differing from those of the other Lycopodiinae (Fig. 204*E*).

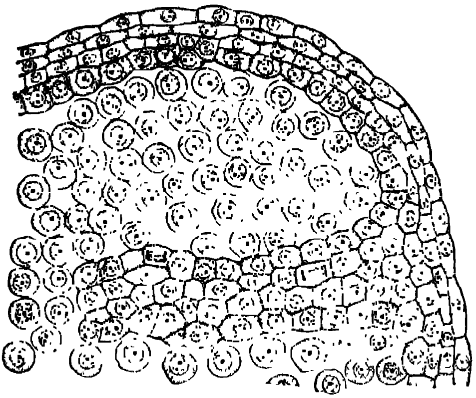

FIG. 202 Cross section of small portion of a microsporangium of *Isoetes nuttallii*, showing the wall, tapetum, a trabecula, and spore mother cells, ×400

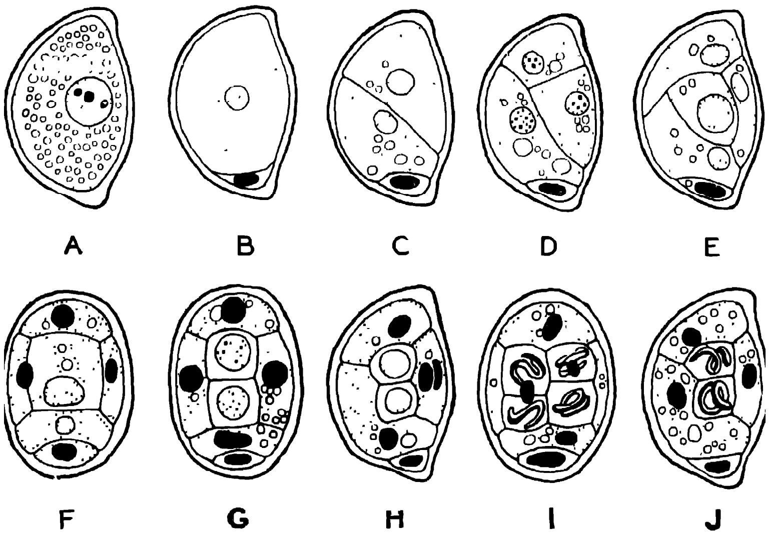

FIG. 203. Male gametophyte of *Isoetes lacustris*. *A*, microspore; *B*, prothallial cell cut off; *C* to *F*, formation of four jacket cells and primary spermatogenous cell; *G* and *H*, division of spermatogenous cell; *I* and *J*, formation of four sperms. *H* and *J* sectioned at right angles to *G* and *I*. (*After Liebig.*)

The female gametophyte develops inside the megaspore and resembles in a general way that of *Selaginella* (Fig. 204*A*). The megaspore is uninucleate when shed. Free-nuclear division occurs, followed by wall formation in the apical region. Then walls fill in the entire megaspore cavity, developing centripetally as in gymnosperms. The female gametophyte does not protrude, as it does in *Selaginella*, but a triradiate crack develops in the megaspore wall along which one or several archegonia and numerous rhizoids appear. In some species the rhizoids are few or wanting. The archegonium is completely embedded. It consists of four tiers of neck cells, a single binucleate neck canal cell, a ventral canal cell, and an egg (Fig. 204*B–D*). No basal cell is formed in development. The archegonium of *Isoetes*, like that of *Selaginella*, represents an advanced type.

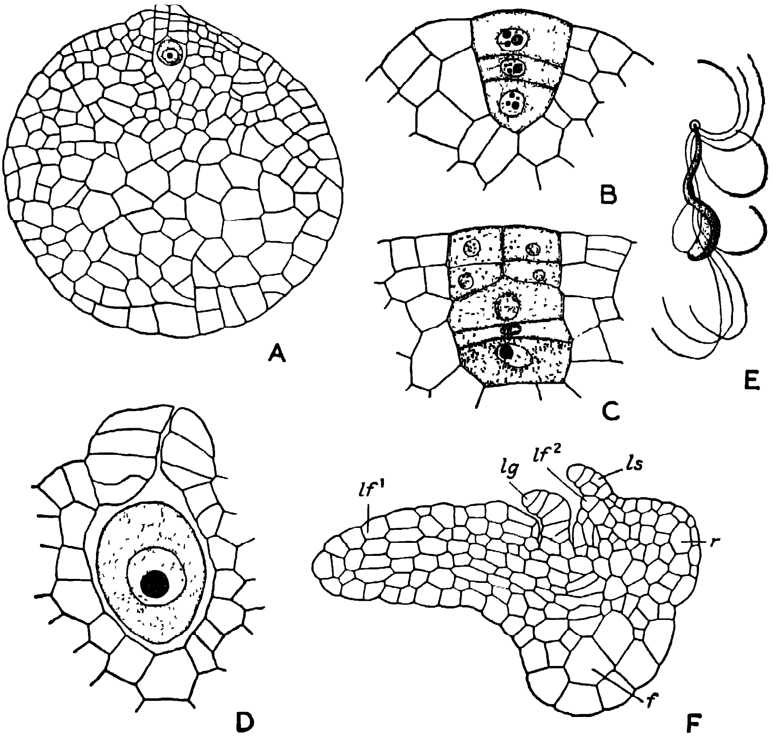

FIG. 204. Female gametophyte and archegonia of *Isoetes echinospora* (*A* to *D*), sperm of *Isoetes malinverniana* (*E*), and embryo of *Isoetes lacustris* (*F*). *A*, female gametophyte with a mature archegonium, the megaspore wall removed, ×140; *B*, young archegonium with primary neck cell, neck canal cell, and primary ventral cell, ×400, *C*, later stage, showing two tiers of neck cells, neck canal cell, ventral canal cell, and egg, ×400; *D*, archegonium with mature egg, ×430; *E*, sperm; *F*, embryo; *f*, foot; *r*, root, lf^1, first leaf; lf^2, second leaf; *lg*, ligule; *ls*, sheath of first leaf. (*A to D*, *after Campbell*; *E*, *after Belajeff*; *F*, *after Liebig*.)

Embryo. The embryo of *Isoetes* differs from that of other living Lycopodiinae in lacking a suspensor. The fertilized egg undergoes a transverse division, but both segments take part in the formation of the embryo proper. A quadrant stage is organized. It seems probable that the two outer cells form the foot, one of the two inner cells the root, and the other inner cell the leaf. As the embryo develops, a greater growth on one side causes it to curve until it finally becomes inverted, the foot lying below and the root and leaf above (Fig. 204*F*). The stem makes its appearance later between the root and leaf. It may originate from either.

Summary. *Isoetes* has an unbranched tuberous stem bearing a relatively few large leaves, each of these having a ligule. The vascular system of the stem is a greatly reduced protostele, amphicribral in organization, and with secondary thickening. A definite strobilus is not organized, unless the whole plant be considered as one. *Isoetes* is heterosporous, the megasporangia producing many megaspores, the microsporangia a much greater number of microspores. Trabeculae are formed in both kinds of sporangia. There is no regular dehiscence. The male gametophyte, formed inside the microspore, consists of a single prothallial cell and a single antheridium, the latter producing four large multiciliate sperms. The female gametophyte, developed inside the megaspore, has considerable vegetative tissue and one to several archegonia. These have only one neck canal cell. The embryo is without a suspensor. Although having a number of characters in common with the other living lycopods, *Isoetes* occupies an isolated position because of its general habit, leaves, multiciliate sperms, and absence of a suspensor.

3. EQUISETINAE[1]

The Equisetinae, like the Lycopodiinae, are a group of ancient origin and were much more abundant and diversified during the Paleozoic than they are today (Fig. 258). They are characterized by jointed, longitudinally fluted stems bearing mostly small, simple leaves arising in whorls and usually united to form a sheath around each node. This cyclic arrangement of leaves is in marked contrast to the spiral arrangement characteristic of other pteridophytes. The sporangia are mostly numerous and borne on the underside of stalk-like *sporangiophores* that are nearly always organized to form a compact strobilus. Of the four orders—the Hyeniales, Sphenophyllales, Equisetales, and Calamitales—only the third has living members.

1. Hyeniales

The Hyeniales are the oldest and most primitive order of Equisetinae, in some respects resembling the Psilophytales. They comprise two

[1] Also called Sphenopsida or Articulatae.

genera, *Hyenia* and *Calamophyton,* both of which lived during the middle Devonian. The aerial shoots were slender and dichotomously branched and, in one species of *Hyenia,* are known to have arisen from a stout horizontal rhizome. The stems were jointed in *Calamophyton* but not in *Hyenia* (Fig. 205). The leaves were small, narrow, and whorled. In *Hyenia* they were forked several times, in *Calamophyton* forked only once. Little is known of the vascular anatomy. The stem of *Calamophyton* was apparently siphonostelic and is thought to have undergone some secondary thickening.

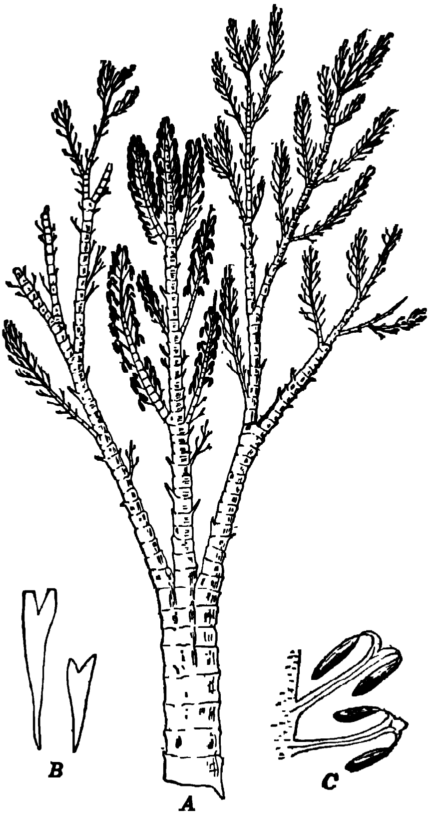

FIG. 205. *Calamophyton primaevum. A,* reconstruction of aerial shoot; *B,* sterile leaves; *C,* sporangiophores. (*After Krausel and Weyland.*)

The sporangia of the Hyeniales were borne on sporangiophores that were grouped to form a loose strobilus in which no bracts were present. In both genera the sporangiophores were once forked, the tip of each division being recurved and bearing two or three pendent sporangia in *Hyenia,* but only one sporangium in *Calamophyton.* Presumably the Hyeniales were homosporous.

2. Sphenophyllales

This is an order of Paleozoic plants ranging from the Devonian to the Triassic. In many respects it is intermediate between the Lycopodiinae and Equisetinae; in fact it is often considered as a separate class of pteridophytes. There are three important genera: *Sphenophyllum, Cheirostrobus,* and *Pseudobornia.*

The slender fluted stem bore whorls of leaves separated by elongated internodes, with branches arising at the nodes (Fig. 206). The leaves, usually six at a node, were mostly simple and wedged-shaped, but were often dichotomously divided into narrow lobes, while in *Pseudobornia* fern-like leaflets were present. The stem, in all cases, was a protostele with exarch xylem and a considerable amount of secondary thickening.

The strobili were terminal and composed of whorled sporophylls showing little or no resemblance to the foliage leaves. In *Sphenophyllum* the bases of the sporophylls were united to form a cup-like sheath, but the tips were free (Fig. 207). The sporangia were borne singly or in pairs on long sporangiophores that arose from the adaxial side of the sporophylls, either singly or several together. The sporangia were pendent from the distal end of the sporangiophore, which was often expanded to form a terminal disk. The strobilus of *Cheirostrobus*, a form genus of Carboniferous age, was more complex than that of *Sphenophyllum*, each sporophyll con-

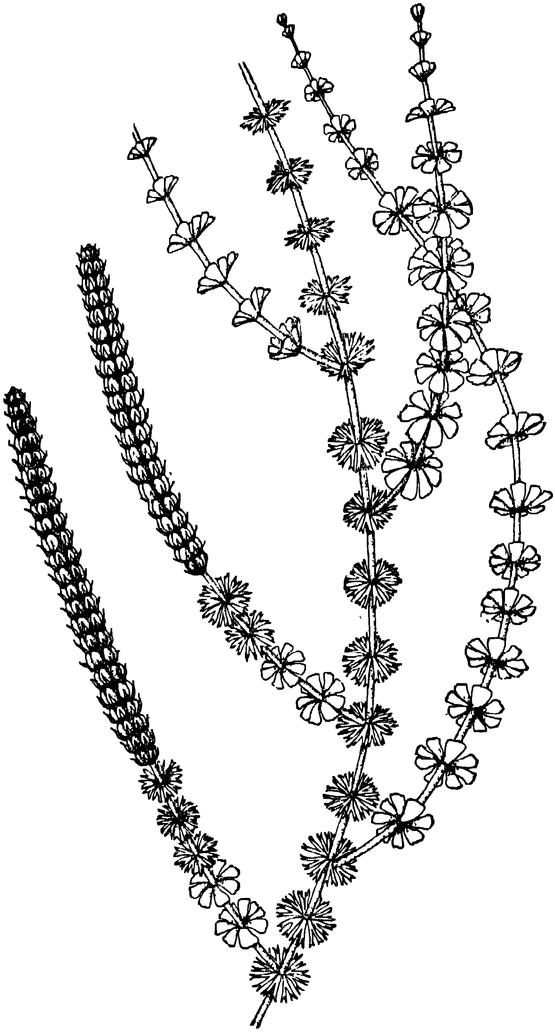

FIG. 206. Reconstruction of the shoot of *Sphenophyllum cuneifolium*, one-third natural size (*From Gilbert M. Smith.*)

sisting of three lower sterile segments arranged in one plane and three upper fertile ones. Each fertile segment was a sporangiophore bearing four sporangia. The strobilus of *Cheirostrobus* was the most complex one in all pteridophytes.

All the Sphenophyllales were homosporous. Nothing is known of the gametophyte generation.

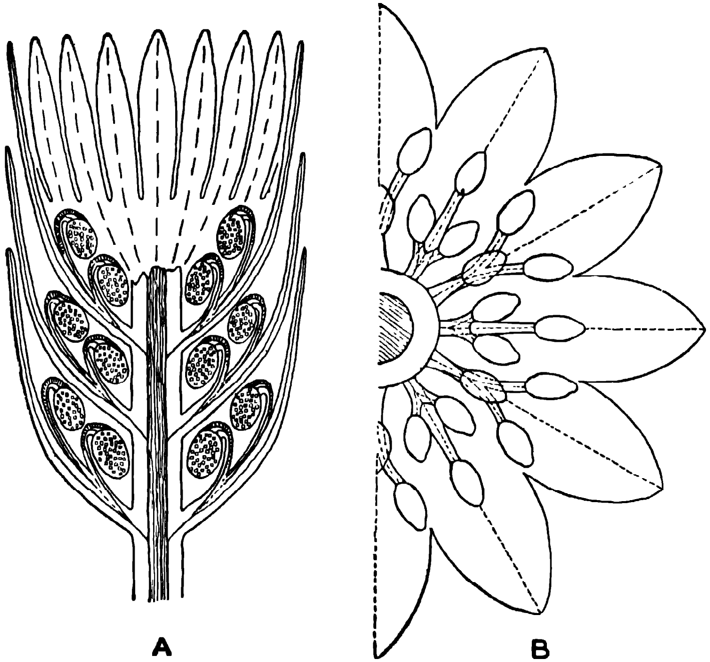

FIG. 207. *Sphenophyllum dawsoni.* *A*, diagram of longitudinal section of cone, showing three whorls of sporophylls and, above, whorl of sporophylls in surface view seen from the inside; *B*, diagram of one-half of a single whorl of sporophylls and sporangiophores. (*A*, *after Scott; B, after Hirmer.*)

3. Equisetales

The Equisetales, often called horsetails, are herbaceous plants comprising a single surviving genus, *Equisetum*, with about 25 species cosmopolitan in distribution. Although related to Paleozoic forms, this order became prominent in the Mesozoic. *Equisetites*, one of the Triassic horsetails, had a stem 20 cm. in diameter and in general was built on a vastly grander scale than modern forms. The common horsetails of temperate regions grow in swamps, meadows, forests, and sandy wastes.

Sporophyte. The largest living species, *Equisetum giganteum*, of tropical America, reaches a height of 12 m. but has a weak stem only about 2 to 3 cm. in diameter at the base. Most of the other species are less than

1 m. tall. The sporophyte of *Equisetum* has a horizontal branching rhizome with whorled leaves at the nodes. It gives rise to erect green shoots that may be either simple or monopodially branched, the branches, like the leaves, arising in whorls (Fig. 208). In some species the shoots branch repeatedly. The stems are longitudinally ridged and grooved, the ridges of one internode alternating with those of the internode immediately above and below. The stems are more or less impregnated with silica, giving them a rough, harsh feel. Roots occur on the rhizome and at the base of the erect stems. They arise in whorls at the nodes.

FIG. 208. Erect shoots of *Equisetum hyemale*. The stems are green, unbranched, and bear whorls of scale-like leaves at the nodes.

The nodes are solid but the internodes have a large central cavity. The aerial stems carry on practically all the work of photosynthesis. The leaves are scale-like, their tips being free but their bases united to form a sheath around the node. The number of leaves at a node corresponds to the number of ridges on the stem, each leaf standing directly above a ridge of the internode directly below it. The stem branches are not axillary but arise at the node alternately with the leaf primordia and at the same level, later breaking through the united leaf bases. Thus the number of branches at a node usually equals the number of leaves. Growth of the root and stem takes place by means of a tetrahedral apical cell that cuts off three rows of lateral segments with striking regularity (Fig. 209).

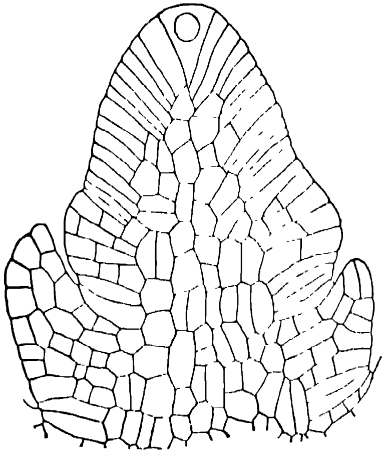

FIG. 209. Median longitudinal tion through the stem tip of *Equisetum arvense*, showing apical cell and its derivatives, ×200.

Vascular Anatomy. The stem of *Equisetum* is characterized by a much-reduced vascular system. The greatest development of xylem occurs at the nodes, where it forms a transverse band. From here a leaf trace goes to each leaf, forming a single median vein. A cross section through an internode shows an extensive cortex bounded externally by an epidermis, a circle of small, isolated, vascular bundles separated from one another by broad bands of parenchyma, and a hollow pith (Fig. 210*A*). The cortex is peculiar in having a ring of large air spaces, called *vallecular canals*, one of which lies beneath each furrow present on the outer surface of the stem.

The epidermis has thick, strongly silicified cell walls. Underlying it is a band of sclerenchyma projecting inward beneath the ridges and sometimes not continuous across the grooves. Green tissue occupies most of the cortical region, occurring largely or entirely beneath the furrows. Stomata, communicating with the green tissue, are situated in the grooves. Their guard cells are peculiar in that each lies inside and next to a subsidiary cell, so that they seem to be double.

Internal to the vallecular canals and alternating with them, and so lying beneath the ridges, are the smaller *carinal canals*, one of which belongs to each vascular bundle. The carinal canals mark the position of the protoxylem, the disorganization of which results in their formation. The metaxylem, which is greatly reduced in amount, lies along the sides of and external to the carinal canals (Fig. 210*B*). It develops centrifugally, a condition designated as endarch. A small group of phloem elements, consisting of sieve tubes and parenchyma, are present. The phloem has a collateral relation to the xylem. No secondary tissues are formed. Generally a continuous endodermis surrounds the ring of vascular bundles, but often an endodermis occurs both inside and outside the bundles. Sometimes each bundle is enclosed by its own endodermis. Although the vascular bundles are small and widely separated, because of

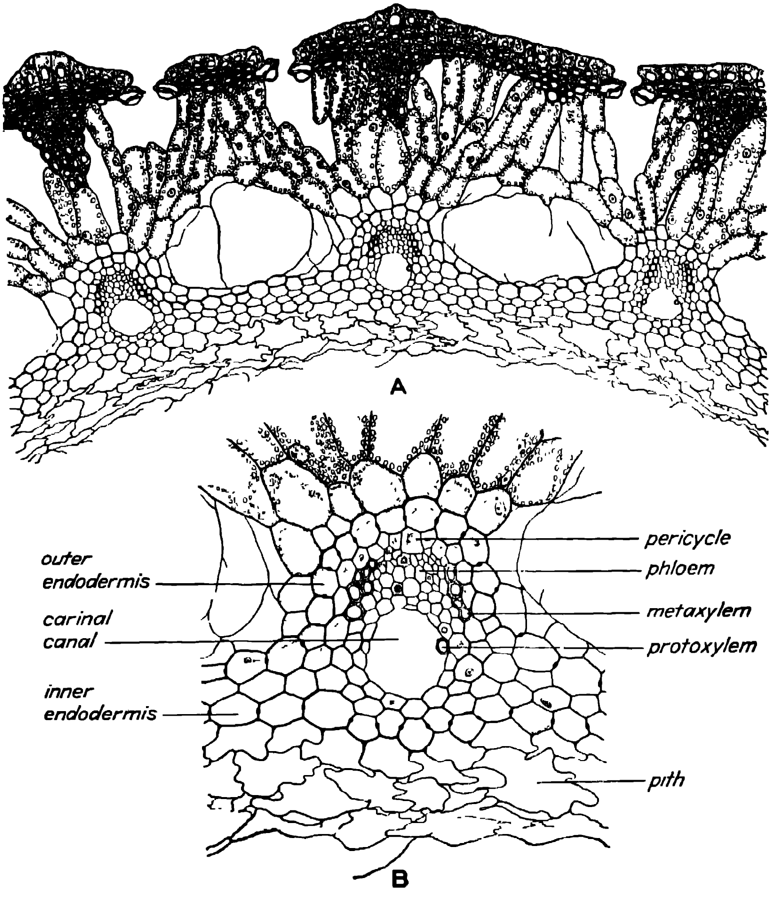

FIG. 210. Stem structure of *Equisetum hyemale* var *intermedium*. *A*, portion of cross section of an internode, showing thick-walled epidermis with three stomata, sclerenchyma, green tissue, two vallecular canals, and three vascular bundles, ×100; *B*, a single vascular bundle, ×250.

their arrangement and the position of the xylem and phloem, the stem of *Equisetum* is an ectophloic siphonostele.

Sporangium. The strobili of *Equisetum* are solitary and terminal on the main stem or sometimes on its branches. Generally they are borne on ordinary green shoots, but in some species they occur on special shoots. In *Equisetum arvense*, for example, there are two kinds of aerial shoots. They arise from the same rhizome but at different times of the year.

The first shoots to appear above ground in the spring are fertile but are unbranched, yellowish brown, and lacking in chlorophyll. They wither soon after the spores are shed. Green, branching, sterile shoots then appear and persist throughout the summer.

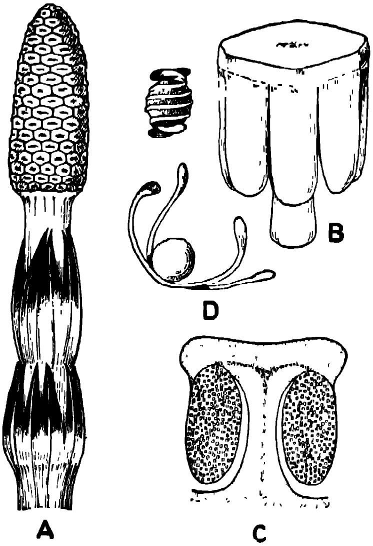

Fig. 211. Spore-bearing structures of *Equisetum arvense*. *A*, terminal portion of fertile shoot with strobilus, natural size. *B*, a single sporangiophore, ×15; *C*, longitudinal section of same, ×15; *D*, two ripe spores, ×150.

The strobilus of *Equisetum* consists of a central axis bearing numerous whorled sporangiophores (Fig. 211*A*). The development of sporophylls is entirely suppressed. Each sporangiophore is peltate and bears 5 to 10 pendent, sac-like sporangia attached to the margin of a six-sided disk. This is supported by a short stalk that arises directly from the axis of the strobilus and is perpendicular to it (Fig. 211*B*, *C*).

The sporangium, which is eusporangiate in development, arises from a single superficial initial and not, as in the Lycopodiinae, from a row of initials (Fig. 212). However, the sporogenous tissue is derived not only from the inner segment that results from the first periclinal division of the initial but also, in part, from the outer segment (Fig. 212*D*). The tapetum is derived from the wall, which becomes several layers thick but, when the sporangium is mature, consists of a single layer of cells, the inner layers breaking down. In contrast to that of the lycopods, the tapetum becomes two- or three-layered and soon disorganizes, forming a *plasmodium* around the spore mother cells. Following the formation of tetrads, the tapetal plasmodium is absorbed by the developing spores. *Equisetum* is homosporous. The spores are unique in containing numerous chloroplasts when ripe and in having, on the outside, two slender bands derived from the outer layer of the spore wall (Fig. 211*D*). These are hygroscopic and assist in spore dispersal. Each band is attached to the spore at its middle, the tips being spatulate. The bands uncoil when dry and wrap around the spore when moist. When the spores are ripe, the axis of the cone elongates slightly, separating the sporangiophores. The sporangia dehisce by means of a longitudinal slit that appears on their inner side.

Gametophyte. The spores of *Equisetum* are short-lived and germinate at once. The gametophyte is usually less than 10 mm. in diameter. It consists of a rounded, cushion-like base of colorless tissue that gives rise to numerous upright lobes of green tissue (Fig. 213*A*). These are irregular, thin, and plate-like. Rhizoids are abundantly produced on the lower surface. The base has a marginal meristem. Both kinds of sex organs are borne on the basal portion of the same prothallium but are seldom present at the same time. The archegonia usually appear before the antheridia. When closely crowded, the prothallia are small and bear only antheridia. For this reason, they were once erroneously regarded as dioecious. The development of the antheridium resembles that of the lycopods (Fig. 213*B*–*E*). The superficial initial divides by a transverse wall, the outer segment producing the sterile jacket and the inner one the spermatogenous tissue. The sperms are large, coiled, and multiciliate.

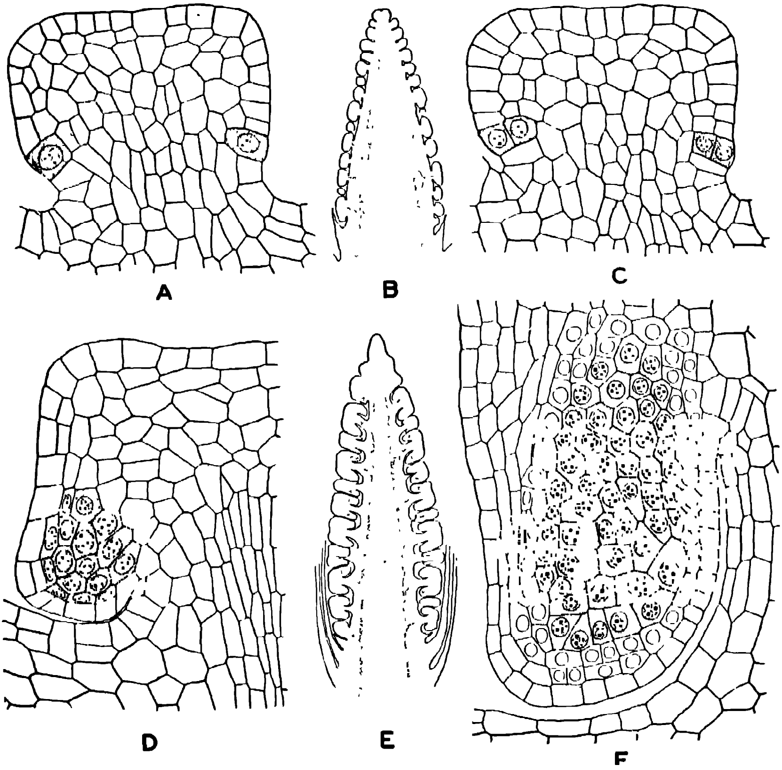

FIG. 212. Early development of the sporangium of *Equisetum arvense*. *A*, longitudinal section of young sporangiophore with two sporangium initials, ×200; *B*, longitudinal section of young strobilus, ×12; *C*, a sporangiophore of same, showing first division of initials, ×200; *D*, longitudinal section of one-half of sporangiophore, showing early differentiation of sporogenous tissue, ×200; *E*, longitudinal section of slightly older strobilus than shown above, ×8; *F*, a sporangium of same, showing further development of sporogenous tissue and differentiation of tapetum, ×200.

The archegonium develops as in other pteridophytes, but no basal cell is formed (Fig. 213*F–H*). It has either one neck canal cell or two of them separated by a vertical wall.

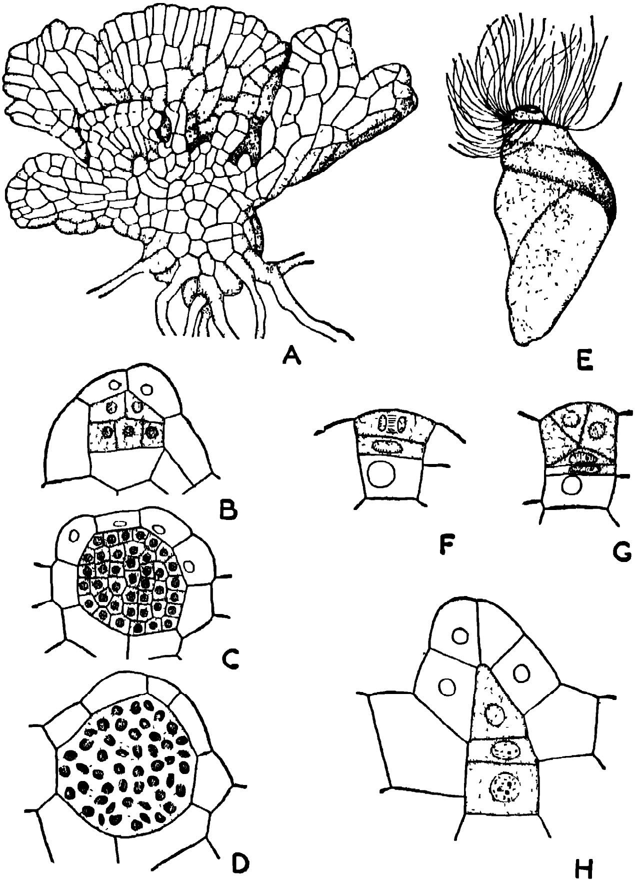

Fig. 213. *Equisetum telmateia.* *A*, gametophyte with archegonia occurring beneath the upright lobes, ×38; *B*, young antheridium, showing sterile jacket and spermatogenous tissue; *C*, slightly older antheridium; *D*, mature antheridium with nearly ripe sperms; *E*, sperm of *Equisetum arvense*; *F*, young archegonium with primary neck cell and central cell; *G*, slightly older archegonium, showing neck cells, primary neck canal cell, and primary ventral cell; *H*, nearly mature archegonium with neck canal cell, ventral canal cell, and egg; *B*, *C*, *D*, ×210; *F*, *G*, *H*, ×325. (*A, after Walker; E, after Sharp; B, C, D and F, G, H, after Gilbert M. Smith.*)

Embryo. The embryo does not have a suspensor. The fertilized egg divides transversely, then into quadrants, the inner segments forming the foot and root, the outer ones the stem and leaf. The stem and root segments soon form an apical cell.

Summary. The elongated, jointed, longitudinally fluted stem bears numerous small, simple, whorled leaves united to form a sheath around

FIG. 214. Portion of restoration of Carboniferous swamp forest in the Chicago Natural History Museum, showing *Calamites* (tree in center) and a fallen trunk of *Sigillaria*. The small plants in the foreground are *Sphenophyllum emarginatum*.

each node. Branches, where present, are also whorled and arise alternately with the leaves. The vascular system of the stem is a much-reduced ectophloic siphonostele with widely separated, endarch, collateral bundles. There is no secondary thickening. All species are homosporous and have a definite strobilus composed of whorled, peltate sporangiophores, each bearing 5 to 10 pendent sporangia with longitudinal dehiscence. Sporophylls are absent. The prothallium is aerial and cushion-like, with erect, green, ribbon-like lobes. The sperms are numerous, large, and multiciliate. The archegonia have one or two neck canal cells. The embryo lacks a suspensor. The Equisetales are a distinct order, superficially unlike any other group of living pteridophytes.

4. Calamitales

This is a Paleozoic order closely related to the Equisetales and often combined with it. It ranged from the Devonian to the Triassic. The principal genus is *Calamites* (Fig. 214). The Calamitales were tree-like forms, some reaching a height of 20 or 30 m. and a diameter of 1 m. The hollow stems bore whorled leaves and branches, the leaves being either free or united at the base. Although mostly small and narrow, the leaves were larger than in modern horsetails, while in *Archaeocalamites* they were large, dichotomously divided into narrow segments, and somewhat fern-like in appearance.

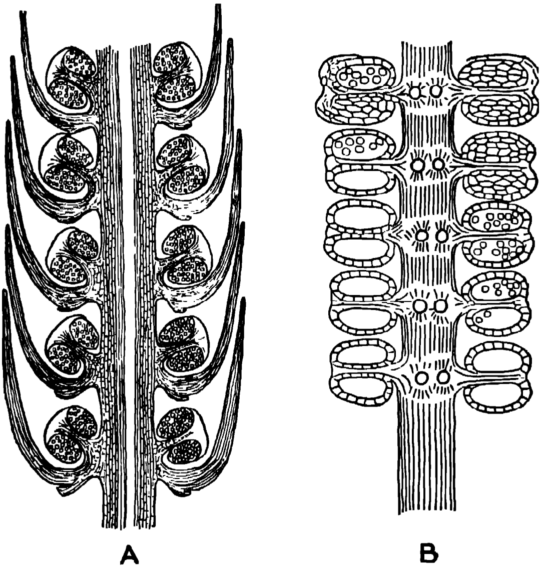

FIG. 215. Longitudinal sections of cones of Calamitales. *A*, *Palaeostachya*, showing peltate sporangiophores in axils of bracts, diagrammatic; *B*, *Archaeocalamites*, showing axis bearing sporangiophores only. (*A*, *after Scott; B*, *after Renault*)

The vascular anatomy was of an advanced type. The stem was an ectophloic siphonostele, the primary xylem occurring in isolated, collateral vascular bundles arranged in a circle around a hollow pith. The bundles were prevailingly endarch but were mesarch in *Protocalamites*. The young stem of the Calamitales was essentially similar to an adult stem of *Equisetum* but became different as a result of secondary thickening, a feature of the group. Generally the primary tissues were surrounded by a continuous cylinder of secondary wood.

The strobili were made up of whorled, peltate sporangiophores resembling those of *Equisetum*, except that each bore only four pendent sporangia. In *Archaeocalamites* the cone consisted entirely of sporangiophores, but in most of the other genera bracts were also present, a whorl of bracts alternating with a whorl of sporangiophores (Fig. 215). These bracts have been interpreted by some botanists as sporophylls. In *Calamostachys* the alternating whorls of bracts and sporangiophores were equidistant, but in *Palaeostachya* the sporangiophores were situated just above each whorl of bracts, *i.e.*, in their axils.

The Calamitales were either homosporous or heterosporous, depending on the species. Many megaspores were produced in each megasporangium. The difference between the two kinds of spores was not so pronounced as in the heterosporous lycopods and ferns. The gametophyte generation is unknown.

CHAPTER VII

PTERIDOPHYTA (CONTINUED)

4. FILICINAE[1]

The ferns constitute the largest and most representative group of pteridophytes of the present day, numbering about 7,800 species. They are widely distributed over the earth, nearly all growing in moist, shady places. Although making their best display in the tropics, both in number of species and in luxuriance of growth, they are also well represented in temperate regions. The branched or unbranched stem usually bears a few large, spirally arranged leaves that are sometimes simple but are generally divided into leaflets. There are no strobili, the sporangia being very numerous on the margin or abaxial side of the leaves, or borne in special structures called sporocarps. The sporangia may be solitary but more commonly are borne in groups.

Like other vascular plants, the Filicinae possess branch, leaf, and root traces that arise from the stele of the stem and pass outward through the cortex. In all the Filicinae, except those with protostelic stems, the departure of a leaf trace causes an interruption in the continuity of the stele, forming a *leaf gap* (Fig. 221). Leaf gaps are present in ferns and seed plants but not in the lower pteridophytes. Branch gaps are present, however, in all vascular plants having siphonostelic stems (except in *Equisetum*).

The Filicinae were well represented in the Paleozoic, but did not hold as dominant a place in the flora as was once thought (Fig. 258). Most of the fossil fern leaves found in Carboniferous deposits belong to the Cycadofilicales, an order of primitive gymnosperms. Some of the Paleozoic ferns may be referred to two orders with living representatives (Marattiales and Filicales), but most of them belong to the Coenopteridales, an extinct order whose relationships to the others are not clear. Living ferns belong to four orders: Ophioglossales, Marattiales, Filicales, and Hydropteridales.

1. Coenopteridales

The Coenopteridales range from the Devonian to the Permian. They are regarded as the most primitive group of Filicinae, in some respects resembling the Psilophytales. These ferns were all of small or medium size. The stems were erect or horizontal and always protostelic. The

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[1] Sometimes combined with the Spermatophyta under the name of Pteropsida.

stele was either circular in outline (Botryopteridaceae) or more or less lobed (Zygopteridaceae). In the most primitive members division of the frond was not limited to one plane and the leaf stalk bore a series of bifurcating branches (Fig. 216). In some cases the differentiation between stem and leaf was imperfect in that no blade was formed.

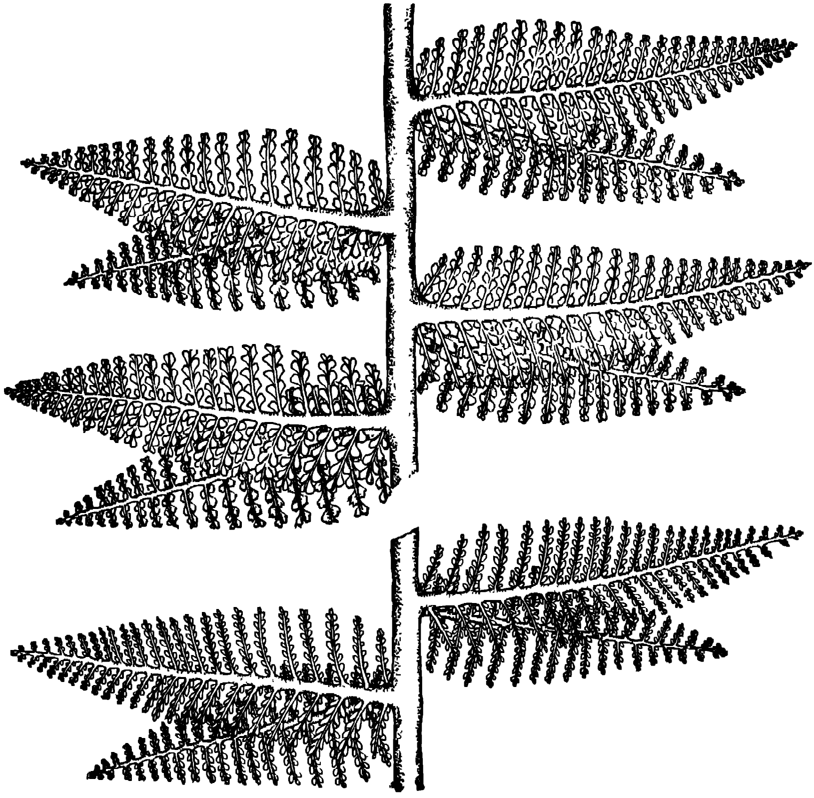

FIG 216. Reconstruction of the leaf of *Etapteris lacattei;* fertile portion above and sterile portion below; one-quarter natural size. (*After Hirmer.*)

The Coenopteridales were eusporangiate and homosporous. The sporangia were large and either terminal or marginal on the ultimate divisions of the frond. Sometimes the sporangia were united to form a synangium-like structure. The output of spores was large. The sporangium wall was more than one layer of cells thick. Dehiscence took place by a terminal pore or a longitudinal slit; in the latter case a rudimentary annulus was present.

2. Ophioglossales

The Ophioglossales comprise 3 genera and about 80 species. *Ophioglossum* and *Botrychium,* each with about the same number of species, are widely distributed, while *Helminthostachys*, with a single species, is confined to Polynesia and tropical Asia. The Ophioglossales are unknown as fossils but constitute the most primitive order of living ferns.

Sporophyte. Most of the Ophioglossales are erect terrestrial plants. The stem is a short, upright, unbranched rhizome producing a few large leaves and numerous rather fleshy roots. Usually only one leaf is formed each year. The smallest species of *Ophioglossum* and *Botrychium* are less than 8 cm. tall, but several species of *Botrychium* may reach a height of 60 cm. *Ophioglossum pendulum*, an epiphyte of the Oriental tropics, has a creeping stem and pendent leaves that are frequently 1.5 m. long. The leaf of *Helminthostachys* is about 30 cm. in length.

FIG. 217. *Ophioglossum californicum*, about one and one-half times natural size.

As a rule, the leaf blade of *Ophioglossum* is simple, while that of *Botrychium* is pinnately divided (Figs. 217 and 218). The leaf blade of *Helmin-*

thostachys is palmately divided. Except in *Botrychium virginianum*, the leaves are fleshy. The blade has many veins that in *Ophioglossum* are reticulate but in the two other genera branch dichotomously and end freely. At the apex of the rhizome is a large bud containing the primordia of leaves that expand during the next four or five seasons. In all genera the stem tip and each successive leaf are ensheathed by the base of the next older leaf. The vernation of the Ophioglossales is not circinate, as in the higher ferns, but erect. Both the root and stem increase in length by means of a tetrahedral apical cell.

FIG. 218. *Botrychium dissectum*, about one-half natural size. (*From Chamberlain.*)

Vascular Anatomy. The leaf blade is simple in structure, with an epidermis enclosing uniform mesophyll. Stomata may occur on both

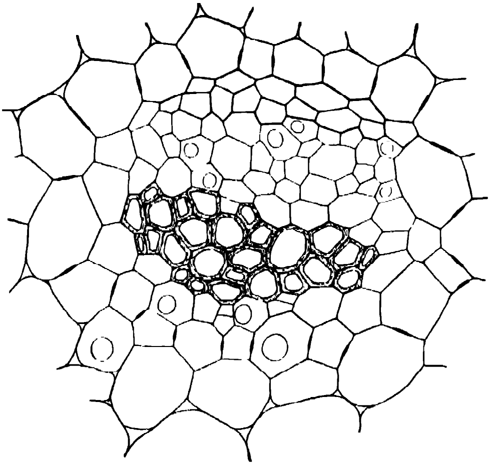

FIG. 219. Cross section of the stelar portion of the root of *Ophioglossum californicum*, showing the thick-walled xylem in contact with the thin-walled phloem, both surrounded by the pericycle and endodermis, ×250

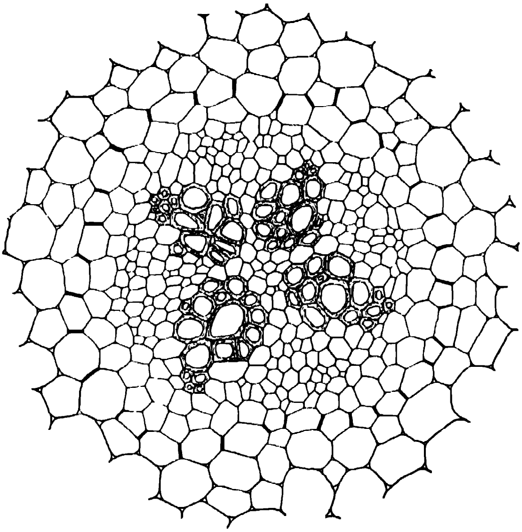

FIG 220. Cross section of the stelar portion of the root of *Botrychium virginianum*, showing four xylem groups, ×150.

sides of the blade or only on the lower side. In *Ophioglossum* the root is very simple in structure, generally having but one xylem group and either one or two phloem groups (Fig. 219). In *Botrychium* the root has two to four xylem groups (Fig. 220), in *Helminthostachys* four to seven. The roots of all genera are exarch and without secondary thickening.

The vascular anatomy of the stem is of an advanced type. In *Botrych-*

ium and *Helminthostachys* the stem is an ectophloic siphonostele, while in *Ophioglossum*, because of the presence of very large, overlapping leaf gaps, the bundles are widely separated and a dictyostele is formed. In all genera the relation of the xylem to the phloem is collateral. The development of the xylem is mesarch in *Helminthostachys* and endarch in the two other genera. A notable feature of *Botrychium* is the presence of a stelar cambium and of marked secondary thickening (Fig. 221).

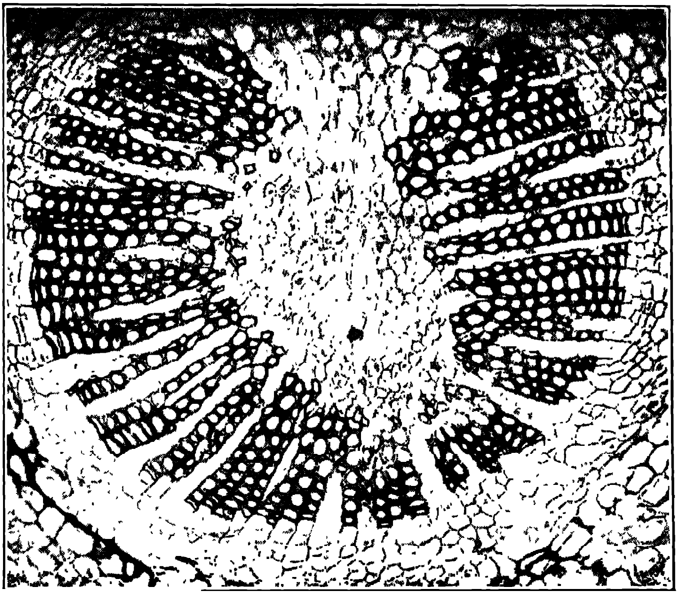

Fig. 221. Cross section of the central portion of the rhizome of *Botrychium virginianum*, an ectophloic siphonostele, ×72. Most of the xylem is of secondary origin.

Although a considerable amount of secondary xylem is formed, there is little or no secondary phloem. The vascular rays are one layer of cells in width. An advanced feature is the occurrence, in *Botrychium* and *Helminthostachys*, of large tracheids with bordered pits instead of the scalariform markings found in other ferns. In *Ophioglossum* the tracheids are reticulate.

Sporangium. All the Ophioglossales are homosporous and eusporangiate. The most distinctive feature of the group is the presence of a "fertile spike," a sporangium-bearing stalk that arises from the basal portion of the leaf as a specialized leaf segment. In *Ophioglossum* the fertile segment is relatively simple, being cylindrical and unbranched, and bearing two lateral rows of sunken sporangia (Fig. 217). Each sporangium does not seem to arise from a single initial cell but from a small group of initials.

In *Botrychium* the fertile segment is more complex than in *Ophioglossum*. In nearly all species it is pinnately branched, the narrow divisions bearing two rows of spherical sporangia that are not embedded but project on a very short stalk (Fig. 218). In development, the sporangia arise separately, each from a single initial. In *Helminthostachys* the fertile segment is spike-like and bears two rows of crowded, oval, stalked sporangia, a number of which may be borne on a single stalk. The vascular anatomy of the leaf and the occurrence of occasional reversions indicate that the fertile segment of *Ophioglossum* and *Botrychium* represents two united basal leaflets, while in *Helminthostachys* it represents a single leaflet.

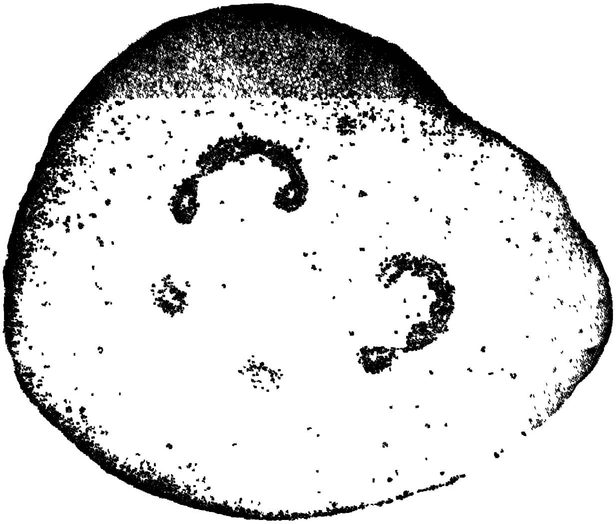

FIG. 222. Cross section of the petiole of *Botrychium virginianum*, ×10.

In almost all the Ophioglossales each leaf trace arises from the stele of the stem as a single strand, but branches before or as it enters the leaf. A cross section of the petiole of *Ophioglossum* shows a single row of vascular bundles arranged in a circle, those on the adaxial side passing into the "fertile spike" and the others going into the sterile blade. The petiole of *Botrychium*, just below the fertile segment, usually displays two pairs of vascular bundles arranged symmetrically on each side (Fig. 222). From the two larger ones, which are crescent-shaped, a pair of smaller bundles branch off and pass into the fertile segment, while at higher levels two small bundles similarly depart to each pair of sterile leaflets.

The sporangium wall, in the Ophioglossales, is about five layers of cells thick. No annulus is formed. The tapetum is probably derived from the innermost layer of wall tissue and may consist of one layer or several layers of cells. In all three genera the tapetum is peculiar in that the protoplasts are liberated from their cells before the spores are in the tetrad stage (Fig. 223). These protoplasts fuse to form a multinucleate plasmodium that surrounds groups of spore mother cells and contributes nourishment to them. These groups break up just prior to the formation of tetrads. The plasmodium disappears as the spores mature. Each sporangium produces a large number of spores. Dehiscence occurs by means of a longitudinal slit in *Helminthostachys* and by a transverse slit in the two other genera.

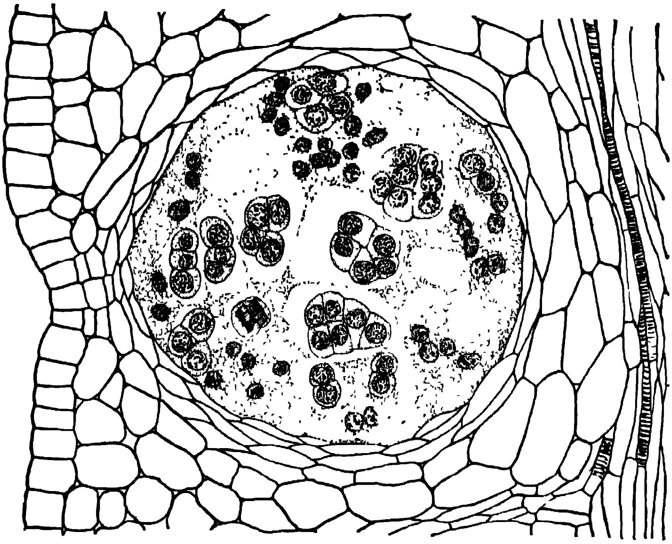

FIG. 223. Longitudinal section through portion of young fertile spike of *Ophioglossum californicum*, showing groups of spore mother cells surrounded by multinucleate plasmodium derived from the tapetum, × 130.

Gametophyte. In all the Ophioglossales the prothallium is subterranean, saprophytic, and without chlorophyll. An endophytic fungus is always present. The prothallium of *Ophioglossum* is cylindrical and either simple or branched (Fig. 224*C*, *D*). It may reach a length, in *Ophioglossum vulgatum*, of 6 cm. Rhizoids are wanting. The antheridia and archegonia are scattered and intermixed. The gametophyte of *Botrychium* is tuberous, dorsiventral, and flattened (Fig. 224*A*). It reaches a length, in some species, of 18 mm., in others, of only 3 mm. The surface may be smooth or covered with rhizoids, according to the species. The antheridia are borne on a median dorsal ridge, while the archegonia, appearing later, form a row on each side of the ridge (Fig. 224*B*). In *Helminthostachys* the prothallium is somewhat similar to that of *Botrychium*, but is more irregular and has a lobed basal portion that gives rise to an upright cylindrical branch bearing sex organs. As in *Botrychium*, the antheridia appear before the archegonia.

The antheridium of the Ophioglossales is large and sunken (Fig. 225*A*, *B*). It develops as in the lower pteridophytes, the spermatogenous tissue arising from the inner segment resulting from a periclinal division of the superficial initial. In *Ophioglossum* the wall remains one-layered, but in the two other genera it becomes two-layered. The sperms are numerous, large, coiled, and multiciliate (Fig. 225*C*). The archegonium initial is also superficial and divides periclinally, the outer cell forming the neck and the inner one giving rise to the central cell and basal cell (Fig. 225*D*–*G*). A basal cell is not present, however, in some species of *Botrychium*. The axial row, derived from the central cell, consists of a

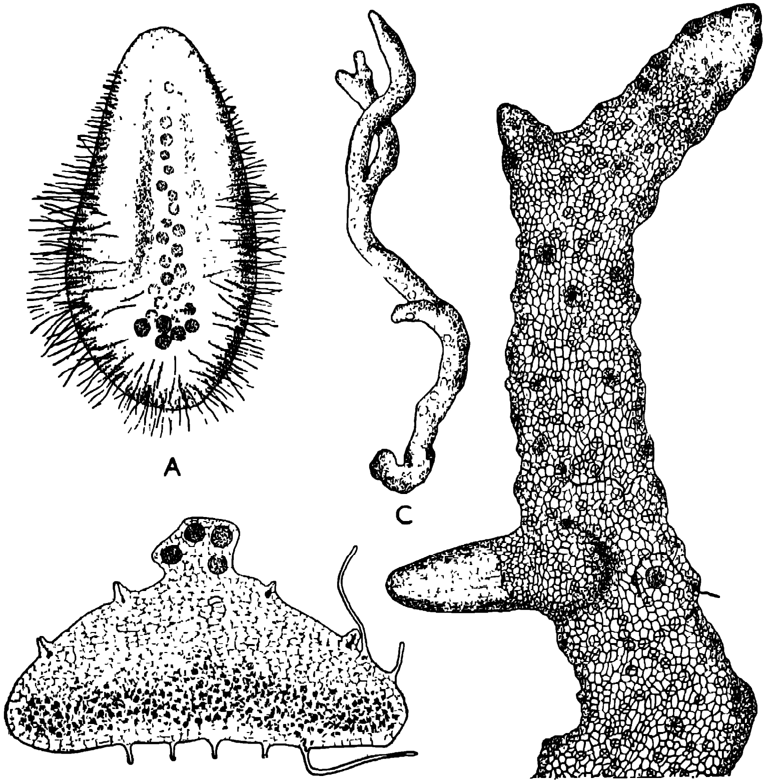

FIG. 224. Prothallia of Ophioglossales. *A*, prothallium of *Botrychium virginianum* with dorsal ridge bearing antheridia, ×16; *B*, cross section of same, showing antheridia on ridge, archegonia on the sides, and fungal zone below, ×17; *C* and *D*, *Ophioglossum vulgatum*; *C*, entire prothallium, about ×2; *D*, one-half of a prothallium with antheridia and archegonia on surface and, to left, a young sporophyte with first root, ×30. (*A and B, after Jeffrey; C and D, after Bruchmann.*)

single binucleate neck canal cell, a very inconspicuous ventral canal cell, and an egg.

Embryo. The embryo of *Botrychium dissectum* and that of *Helminthostachys* are unique in that a suspensor is developed, but in all the other

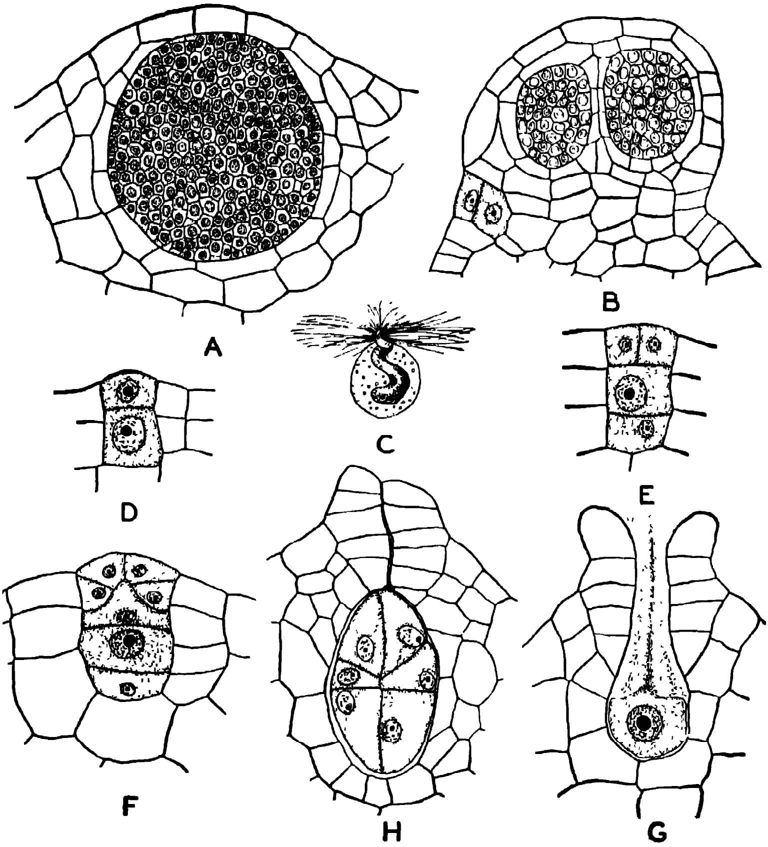

FIG. 225 Sex organs of Ophioglossales. *A*, antheridium of *Ophioglossum vulgatum*, ×150; *B*, antheridia of *Botrychium virginianum*, ×200, *C*, sperm of *Ophioglossum; D* to *G*, development of archegonium of *Ophioglossum vulgatum*, ×225; *D*, first division of initial; *E*, young archegonium with two neck cells, central cell, and basal cell; *F*, later stage, showing division of central cell; *G*, mature archegonium, *H*, young embryo of *Botrychium virginianum*, ×250. (*B and H, after Jeffrey; others after Bruchmann.*)

Ophioglossales none is present. The first wall in the fertilized egg is transverse and usually a quadrant stage is formed, but the subsequent divisions are irregular and rather indefinite (Fig. 225*H*). The embryonic organs are differentiated rather late, and so it is not possible to assign them to definite quadrants. The entire inner portion of the embryo forms the foot, while the outer portion gives rise to the root, stem, and leaf. Generally the root arises first and grows considerably before the other organs are differentiated. The leaf is the last member to appear.

Summary. The Ophioglossales are homosporous and eusporangiate. The sporangia are borne on a characteristic "fertile spike," which probably represents a single leaflet in *Helminthostachys* and two united basal leaflets in *Ophioglossum* and *Botrychium.* The sporangium wall is several layers of cells thick and is without an annulus. The leaves are erect in vernation, not circinate. The gametophyte is subterranean, saprophytic, and without chlorophyll. It contains an endophytic fungus. The antheridium develops as in the other eusporangiate pteridophytes. The inner portion of the embryo forms the foot, the outer portion the root, stem, and leaf. The Ophioglossales have a number of distinctive features. The vegetative structure of the sporophyte is advanced, but the spore-producing structures and the gametophyte are primitive. The order may have been derived from the Coenopteridales, but does not seem to have given rise to any other modern group.

3. Marattiales

The Marattiales are an ancient order of ferns extending back into the Paleozoic. In certain respects they are intermediate between the Ophioglossales and Filicales. Although once widespread and abundant, they are represented today by only 7 genera and about 55 species almost exclusively tropical in distribution. The largest genus is *Angiopteris,* with 25 species. It is found only in the Eastern Hemisphere. Two other important genera, each with about 13 species, are *Marattia,* occurring in tropical regions throughout the world, and *Danaea,* confined to tropical America. The four other genera, each with a single species, are confined to southern Asia.

Sporophyte. The Marattiales are mostly large ferns with thick fleshy leaves (Fig. 226). In most species of *Danaea* the stem is creeping and occasionally branched, but in nearly all other members of the order it is short, stout, erect, and unbranched. The stem is always covered with persistent leaf bases. The roots are thick and fleshy and the leaves, which in *Angiopteris* may exceed 5 m. in length, are in nearly all cases pinnately divided. A peculiarity of the group is the occurrence of a pair of fleshy stipules at the base of each leaf. The venation is dichotomous and open except in one genus (*Christensenia*), where it is reticulate. The vernation is circinate throughout the order. Elongation of the root and stem takes place by means of a meristem, an apical cell being present only in young plants. In possessing an apical meristem, the Marattiales differ from all other ferns.

Vascular Anatomy. A cross section through a leaf reveals an epidermis on both surfaces, with stomata present only below. Palisade tissue is

FIG. 226. *Angiopteris evecta.* (*From Wettstein.*)

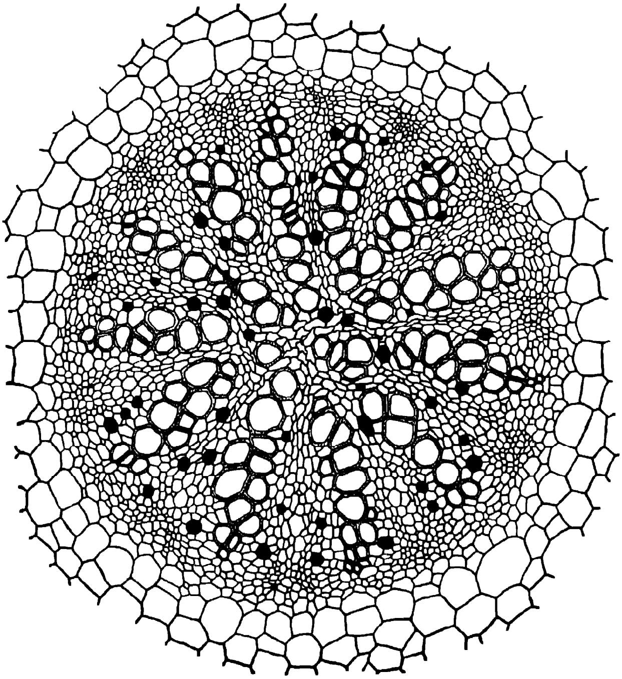

FIG. 227. Cross section of the stelar portion of the root of *Marattia*, an exarch radial protostele with many protoxylem points, ×75.

developed beneath the upper epidermis, the rest of the mesophyll consisting of spongy tissue. The roots of the Marattiales are characterized by a large number of protoxylem points (Fig. 227). The xylem is usually lignified to the center.

The vascular anatomy of the stem is very complex. The cortex consists of parenchyma containing mucilage canals, but no sclerenchyma is present. The vascular cylinder is a dictyostele with large overlapping leaf gaps and widely separated bundles. The latter, in all genera, are amphicribral (phloem surrounding the xylem) and either mesarch or endarch in development. In *Danaea* the vascular bundles are seen, in a cross-sectional view of the stem, to be arranged in a single circle surrounding the pith. In *Marattia* the stem is more complex in that two concentric circles of bundles are present, while in *Angiopteris*, where the stem reaches its greatest degree of complexity, there is a series of four or five circles of vascular bundles. In all the Marattiales the stem bundles undergo more or less branching and fusion, and commissural strands, connecting certain parts of the vascular system with one another, arise inside the dictyostele. Secondary thickening does not occur. As in the higher ferns, the tracheids are scalariform.

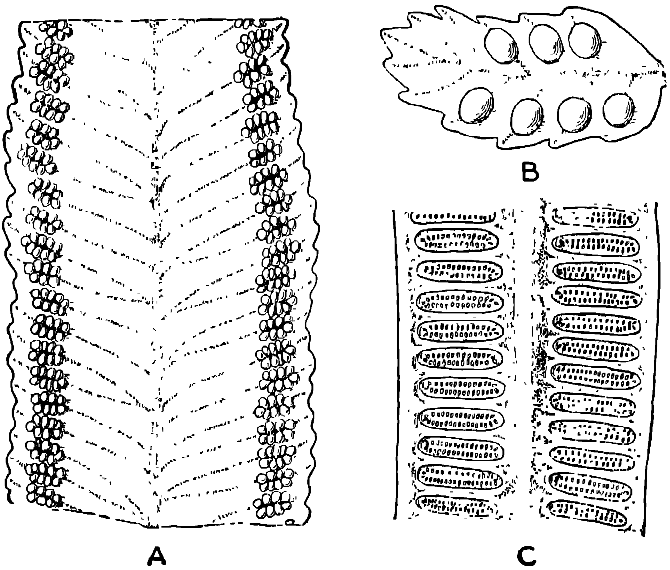

FIG. 228. Portion of leaflet of *Angiopteris* (*A*) with sori, leaflet of *Marattia* (*B*) with oval synangia, and portion of leaflet of *Danaea* (*C*) with elongated sunken synangia, ×3.

Sporangium. The Marattiales resemble the Ophioglossales in being homosporous and eusporangiate, in having a sporangium wall consisting of several layers of cells, and in lacking an annulus. The sporangia, however, are not borne in a "fertile spike" but on the abaxial side of the leaves. Generally the fertile and sterile leaves are alike in form, but in *Danaea* they are different. The sporangia are sessile and borne in distinct sori, these being generally in two rows. In *Angiopteris* the sporangia are free (Fig. 228*A*), but in *Marattia* and *Danaea* they are united to form *synangia.* The synangia of *Marattia* are superficial, oval, or rounded, and borne near the ends of the veins (Fig. 228*B*). The synangia of *Danaea* are sunken, linear, and borne along the veins; they cover almost completely the backs of the fertile leaflets (Fig. 228*C*).

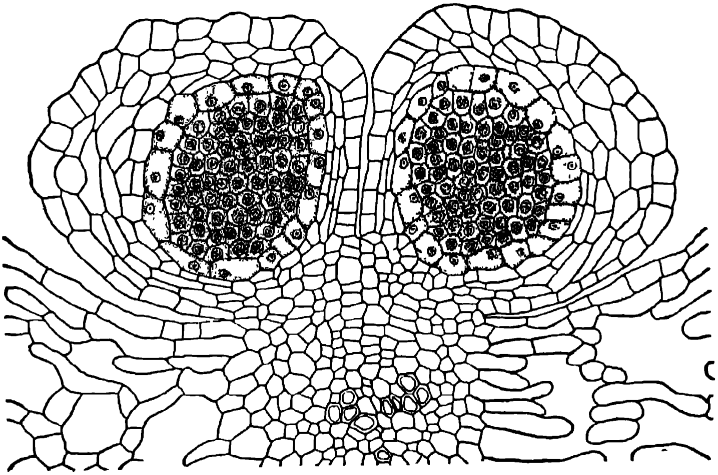

FIG. 229. Section through two sporangia of *Angiopteris evecta,* showing wall, tapetum, and sporogenous tissue, ×200.

All the sporangia in a sorus originate at the same time, each arising from a single initial cell. The sporogenous tissue is differentiated early and, from the cells immediately surrounding it, the tapetum, consisting of one or two layers, is derived (Fig. 229). The tapetum breaks down when the spore tetrads are formed, its substance being absorbed by the developing spores. It does not form a plasmodium. The sporangium of the Marattiales is a relatively large structure, producing a great many spores (1,500 to 7,000). A rudimentary annulus is present in *Angiopteris,* but there is none in *Marattia* and *Danaea.* Dehiscence takes place by means of a median slit or, in *Danaea,* by a terminal pore.

Gametophyte. The Marattiales have a comparatively large gametophyte, sometimes reaching a length of 3 cm., and consisting of a flat, dark green thallus that may be heart-shaped, orbicular, or irregularly lobed. It resembles the gametophyte of the Filicales except that it is relatively thick, long-lived, and, as in the Ophioglossales, provided with an endophytic fungus. The median portion of the prothallium forms a thick cushion. Rhizoids arise from the ventral surface; in *Angiopteris* and *Marattia* they are unicellular, but in *Danaea* they are septate. The antheridia occur on both the upper and lower surfaces of the prothallium, but the archegonia are confined to the lower side, where they are borne on the thickened median portion. Both antheridia and archegonia are sunken. They develop as in the Ophioglossales (Figs. 230 and 231). In the archegonium a basal cell is usually formed in *Marattia* but not in *Angiopteris* and *Danaea*. There may be either two neck canal cells or a single binucleate one. As in all ferns, the sperms are coiled and multiciliate.

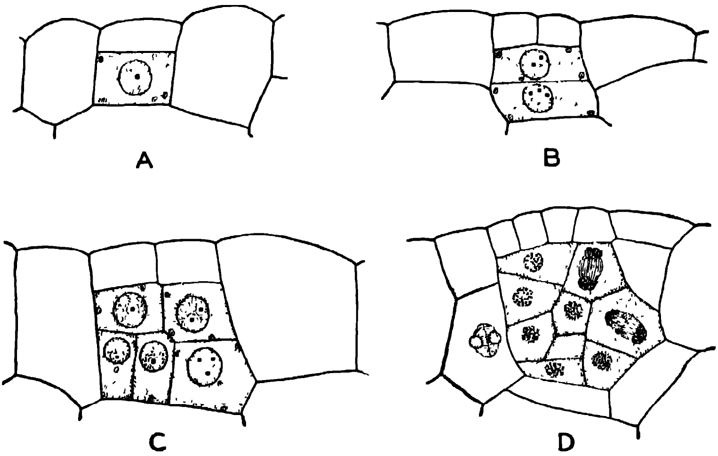

FIG. 230. Early stages in the development of the antheridium of *Angiopteris evecta*, ×350 *A*, division of antheridial initial into primary wall cell and primary spermatogenous cell; *B*, anticlinal division of primary wall cell and periclinal division of primary spermatogenous cell, *C*, further divisions of spermatogenous cells; *D*, slightly later stage, showing completion of antheridial wall by cutting off of a layer of cells from adjacent cells of the prothallium. (*After Haupt.*)

Embryo. The development of the embryo is unlike either that of the Ophioglossales or of the higher ferns. The first division of the fertilized egg is transverse and a quadrant stage is organized. The two outer segments (those next to the neck of the archegonium) give rise to the foot, the two inner ones to the stem and leaf, the leaf arising from the segment nearer the apical region of the prothallium. The root appears later from the inner portion of the embryo. A suspensor has been observed in some species of *Danaea* and exceptionally in *Angiopteris*.

Summary. Like the Ophioglossales, the Marattiales are homosporous and eusporangiate, but the sporangia are borne on the abaxial side of the leaves, usually in synangia. The sporangium wall consists of several layers of cells and is without a definite annulus. The vernation is circinate. The leaves have a pair of fleshy stipules. The gametophyte is flat, green, and aerial. It is relatively thick and contains an endophytic fungus. The development of the antheridium is like that of the Ophioglossales. The inner portion of the embryo forms the stem, leaf, and root,

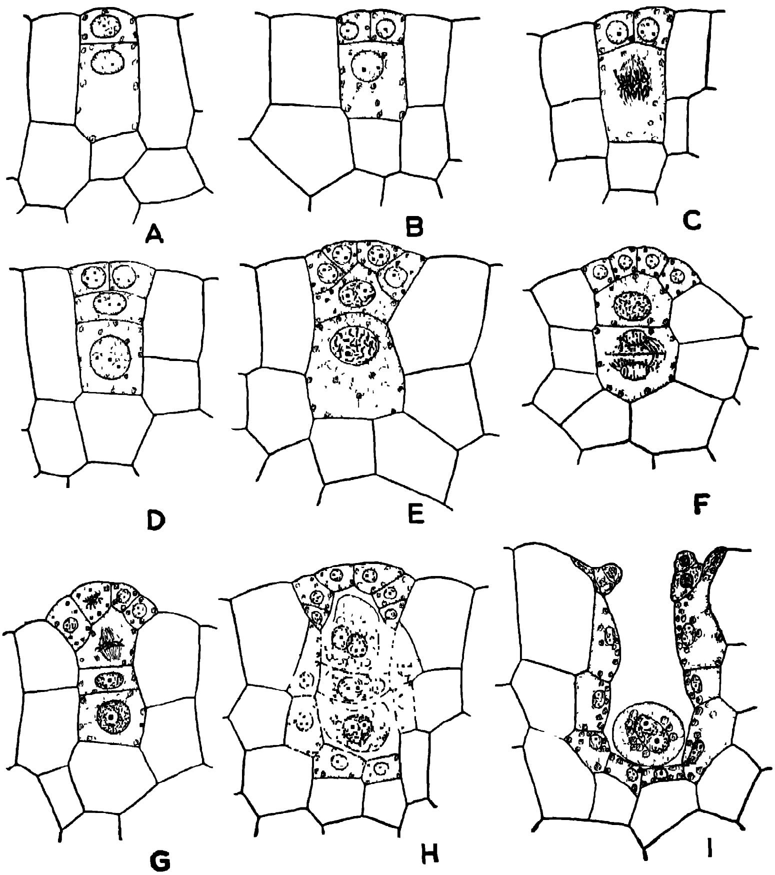

FIG. 231. Development of the archegonium of *Angiopteris evecta*, ×350. *A*, division of archegonium initial into primary neck cell and central cell, *B*, anticlinal division of primary neck cell, *C* and *D*, periclinal division of central cell to form neck canal cell and ventral cell; *E*, formation of two tiers of neck cells; *F*, division of ventral cell to form ventral canal cell and egg; *G* and *H*, formation of a single binucleate neck canal cell, of three tiers of neck cells, and of the sterile jacket; *I*, mature archegonium with egg ready for fertilization (*After Haupt.*)

the outer portion the foot. The Marattiales have characters in common both with the Ophioglossales and the Filicales and, in their degree of complexity, occupy a position between them. These three orders do not form a phylogenetic series. Instead, they seem to have been derived independently from a common ancestry.

4. Filicales

The Filicales constitute by far the largest order of modern ferns, including 12 families, about 170 genera, and approximately 7,600 species. They make their greatest display in the tropics, but are also well represented in temperate regions. The fossil record of the two most primitive families (Osmundaceae and Schizaeaceae), and possibly of a third one (Gleicheniaceae), extends back into the Paleozoic, but that of the other families does not reach beyond the Mesozoic.

FIG. 232. *Gleichenia costaricensis*, photographed near the summit of the Poás volcano in Costa Rica.

Families. The Filicales comprise 7 principal families and 5 small ones of minor importance. All of them have living representatives. The chief families are as follows:

1. *Osmundaceae.* This is the most primitive family. It comprises 3 genera and about 20 species and occurs in both temperate and tropical regions. *Osmunda* is the principal genus, including over one-half the species. It is widely distributed, three species being found in temperate parts of North America.

2. *Schizaeaceae.* This primitive family, including 4 genera and about 160 species, is chiefly tropical. *Schizaea* and *Lygodium* are widely distributed. *Anemia*, the largest genus, is found in tropical America, while *Mohria* is confined to eastern Africa. The family is represented in the Eastern and Southeastern United States by two species of *Schizaea*, one of *Lygodium*, and two of *Anemia*, all of which are rare.

3. *Gleicheniaceae.* This small family of about 130 species includes 3 genera, of which *Gleichenia*, with all the species but two, is of greatest importance (Fig. 232). It is confined to the tropics and subtropics of both the Eastern and Western Hemispheres.

FIG 233. *Dicksonia antarctica*, a tree fern cultivated in the Huntington Botanical Gardens at San Marino, California.

4. *Hymenophyllaceae.* These are the "filmy ferns," small delicate forms chiefly tropical in distribution. There are about 400 species, nearly equally divided between *Hymenophyllum* and *Trichomanes*. Two species of *Trichomanes* are found in the Eastern United States.

5. *Dicksoniaceae.* To this group belong 9 genera and about 125 species mainly tropical in distribution. The chief genera are *Dicksonia*, *Cibotium*, and *Dennstaedtia*.[1] The first two are arborescent (Fig. 233). One species of *Dennstaedtia* is found in the Eastern United States.

6. *Cyatheaceae.* This is a family of tree ferns, including 3 genera and about 700 species. Here belong *Cyathea*, *Alsophila*, and *Hemitelia*, all large genera widely distributed throughout the tropics.

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[1] The position of this genus is uncertain. It is often placed in the Polypodiaceae.

7. *Polypodiaceae.* The Polypodiaceae constitute the highest and largest family of true ferns. Although chiefly tropical, it includes nearly all the ferns of temperate regions. About 150 genera and 6,000 species are known. The following list includes most of the large genera: *Pteris, Adiantum, Athyrium, Cheilanthes, Dryopteris, Polystichum, Asplenium, Blechnum, Elaphoglossum,* and *Polypodium.*

Sporophyte. The sporophyte of the Filicales displays great variation in size, ranging from small delicate herbs to trees 18 m. or more in height. Most members of the group are terrestrial, but some are climbing, some epiphytic, and a few aquatic. The stem may be subterranean or aerial, erect or horizontal, and branched or unbranched. In most true ferns, and in all the common species of temperate regions, the stem is a creeping rhizome without aerial branches. The leaves of tropical species are evergreen. Those of temperate species, with few exceptions, die at the end of the growing season, new ones appearing each spring. The tree ferns of tropical regions have an erect, woody, unbranched stem bearing a terminal cluster of large leaves (Fig. 233).

Some true ferns have simple leaves but most of them have large, characteristic, pinnately divided leaves often called *fronds.* Their leaflets, termed *pinnae,* are usually again divided, the smaller segments being known as *pinnules.* The leaves are generally firm and leathery but are often thin and membranaceous, being very delicate in the "filmy ferns" (Hymenophyllaceae). Stipular wings are present at the base of the petiole in the Osmundaceae but not in the other families. In unfolding from the bud, the leaves uncoil from the base toward the apex and continue to grow at the tip until they have reached their full size. This familiar behavior, known as *circinate vernation,* is very characteristic. The leaves have an elaborate system of branching veins, the branching being nearly always dichotomous and open, but sometimes reticulate (Fig. 240). Branching of the rhizome is usually monopodial but occasionally dichotomous; that of the roots is always monopodial.

In nearly all the Filicales the root tip displays a large tetrahedral apical cell that undergoes very regular segmentation, cutting off cells from the three sides and also from the forward face to form the root cap (Fig. 234). The stem tip likewise grows by means of a large apical cell that nearly always is tetrahedral, cutting off segments in regular succession, but only from the three lateral faces. In the bracken (*Pteridium aquilinum*) a modified form of dolabrate apical cell is present, forming segments right and left.

Vascular Anatomy. The anatomy of the roots and leaves is essentially similar to that of the spermatophytes. The leaves have an upper and a lower epidermis with stomata usually confined to the lower surface, mesophyll, and vascular bundles. As a rule, the mesophyll is uniform. In nearly all the Filicales the root has a stele with two protoxylem groups.

The stems of the Filicales display four different stelar types, being either a protostele, an amphiphloic siphonostele, an ectophloic siphonostele, or a dictyostele. The dictyostele is the most common as well as the most advanced type, but the amphiphloic siphonostele is also of rather frequent occurrence. The other two types are uncommon.

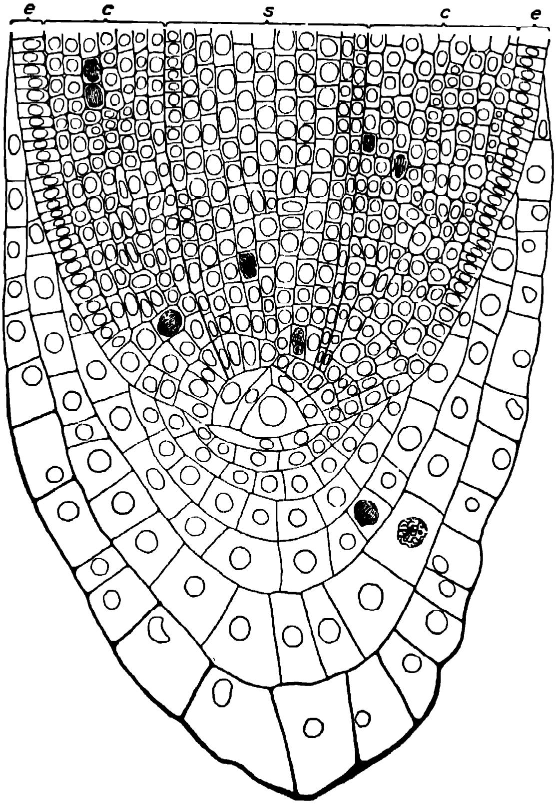

Fig. 234. Median longitudinal section through the root tip of *Pteris gigantea*, showing tetrahedral apical cell from which all the other cells have been derived; *e*, epidermis; *c*, cortex; *s*, stele. (*After Hof.*)

The protoxylem consists of spiral tracheids—elongated cells with spiral thickenings on their walls. The metaxylem is made up almost entirely of scalariform tracheids. These are elongated cells, pointed at each end, with transverse bands of thickening resembling the rungs of a ladder. In nearly all the Filicales the development of the wood is mesarch, the protoxylem being surrounded on all sides by the metaxylem (Fig. 239). Generally the phloem surrounds the xylem, the vascular tissues thus showing an amphicribral arrangement. Sclerenchyma is usually prominently developed. There is no secondary thickening, even in the tree ferns.

Except in protostelic stems, prominent leaf gaps are formed in connection with the departure of leaf traces, as in all the orders of Filicinae. In addition to leaf gaps, perforations not related to the departure of leaf traces are sometimes developed in the vascular cylinder, especially in ferns with elongated rhizomes. In many forms accessory vascular strands are present, usually inside the vascular cylinder. In the common bracken (*Pteridium aquilinum*) we have a well-known example of the occurrence of medullary strands combined with a considerable amount of perforation of the vascular cylinder (Fig. 238). Accessory vascular strands are present also in many tree ferns.

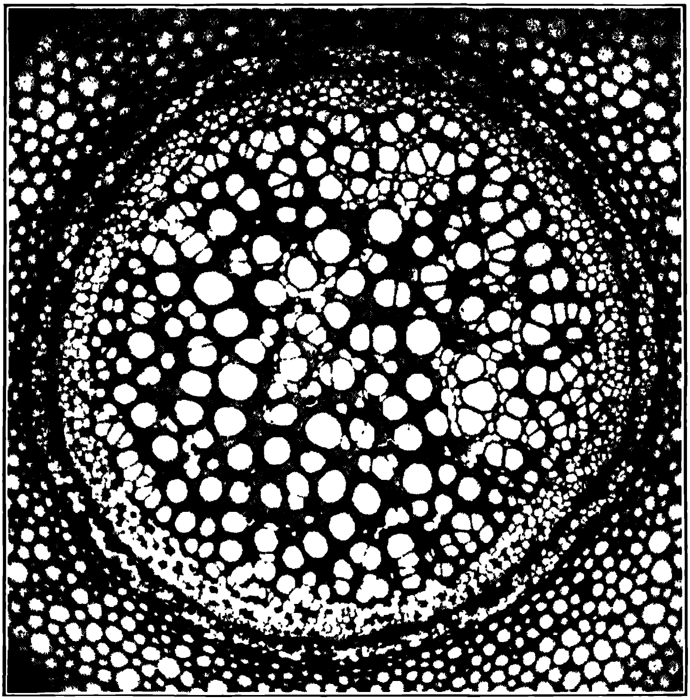

Fig. 235. Cross section of the central portion of the rhizome of *Gleichenia costaricensis*, a protostele, ×50.

Protostele. The protostele, representing the most primitive vascular type, is found only in a few genera, such as *Lygodium*, *Gleichenia*, *Hymenophyllum*, and *Trichomanes;* but it occurs as the earliest developmental stage in most other true ferns.

Gleichenia displays a typical protostele (Fig. 235). No pith is present.

the xylem occupying the center of the stem. A cross section of the rhizome shows a more or less sclerenchymatous cortex, a continuous and distinct endodermis, a several-layered pericycle, and a narrow but continuous band of phloem. The xylem forms a solid central mass consisting of groups of large scalariform tracheids intermixed with parenchyma. Numerous mesarch protoxylem groups are scattered throughout the metaxylem. Leaf traces are connected directly with the stele, forming no gaps.

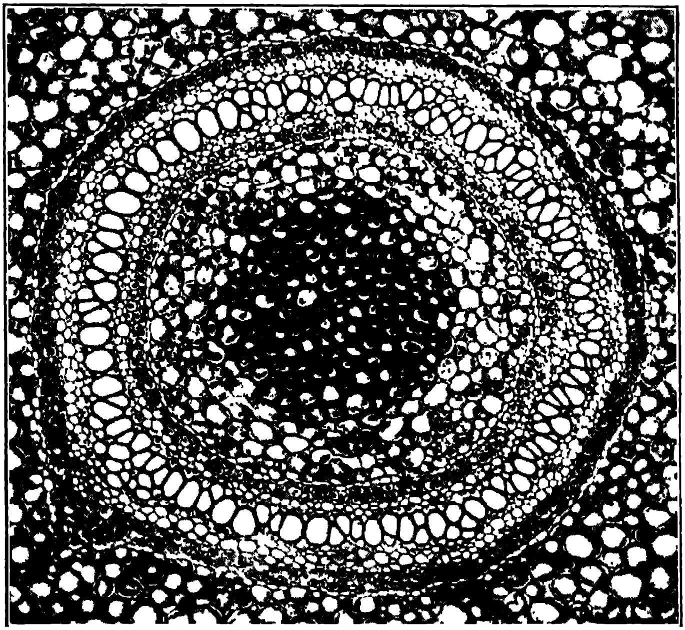

FIG. 236. Cross section of the central portion of the rhizome of *Dennstaedtia punctilobula*, an amphiphloic siphonostele, ×80. In the center of the pith is a group of thick-walled sclerenchyma fibers.

Amphiphloic Siphonostele. This stelar type may be seen in such well-known ferns as *Adiantum* and *Dennstaedtia,* as well as in a number of others. Here the vascular tissues form a cylinder enclosing a pith, the xylem being surrounded both externally and internally by a complete zone of phloem (Fig. 236).

A transverse section of the rhizome of *Dennstaedtia punctilobula,* the hay-scented fern of the Eastern United States, shows a thick outer cortical region composed of dark-colored sclerenchyma and a thin inner parenchymatous region. An outer endodermis delimits the cortex from the outer pericycle, which consists of two or three layers. Next come the outer phloem, the xylem, the inner phloem, the inner pericycle, the inner endodermis, and the pith. Both the outer and inner phloem are made up almost entirely of sieve tubes but are separated from the xylem by a small amount of parenchyma. The xylem forms a narrow cylinder composed of scalariform tracheids. Apparently no protoxylem is present. The inner pericycle usually comprises only one or two layers. The outer portion of the pith consists of parenchyma, the central part of sclerenchyma. The continuity of the vascular cylinder is interrupted by the departure of leaf traces and the gap formed by each is closed above before the next trace is given off. The endodermis is continuous around the margins of the leaf gaps. Because the internodes are shorter in the rhizome of *Adiantum*, the leaf gaps are more numerous. Furthermore, the woody cylinder is wider and consists of both tracheids and parenchyma.

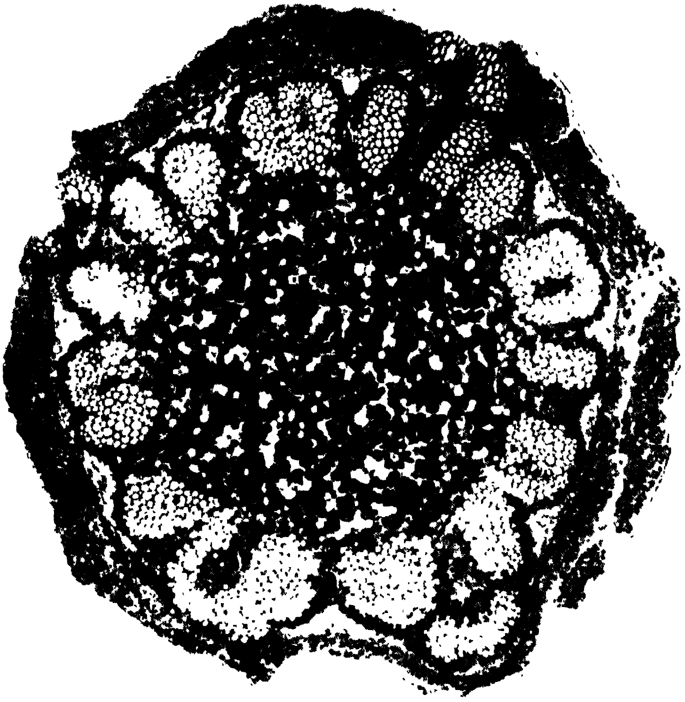

FIG. 237. Cross section of the central portion of the rhizome of *Osmunda cinnamomea*, an ectophloic siphonostele, × 19.

Ectophloic Siphonostele. The ectophloic siphonostele differs from the amphiphloic in lacking internal phloem. Although found in *Schizaea*, it can be seen to better advantage in *Osmunda*. Here the rhizome is covered with persistent overlapping leaf bases. The outer cortex is extensive and consists mainly of dark-colored sclerenchyma, while the inner cortex is narrow and parenchymatous. The endodermis is distinct and continuous, even where the stele is interrupted by the outward passage of leaf traces. The pericycle consists of one to four layers of parenchyma forming a complete sheath. As seen in cross section, the vascular cylinder of *Osmunda* consists of a ring of mesarch xylem strands separated by parenchymatous "rays" that pass outward from the large pith (Fig. 237). In some species the pith may contain sclerenchyma. Surrounding the xylem is a continuous layer of phloem made up chiefly of sieve tubes, while between the xylem and phloem are several layers of elongated parenchymatous cells continuous with the "rays." The xylem really consists of a cylindrical network forming a hollow cylinder, the meshes or "rays" being leaf gaps.

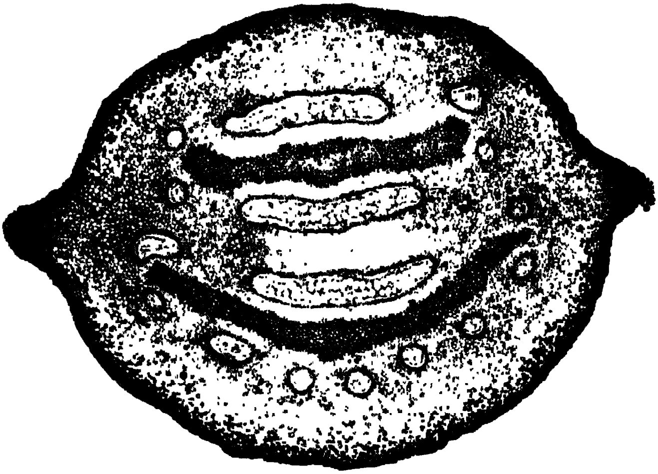

FIG 238. Cross section of the rhizome of *Pteridium aquilinum*, a dictyostele in which the vascular cylinder encloses two or more medullary bundles and two bands of dark, heavy-walled sclerenchyma fibers, ×8.

Dictyostele. Among the lower families of Filicales, a dictyostele is present in *Mohria* and most species of *Anemia*, both members of the Schizaeaceae. Dictyostelic stems are also found in some of the Dicksoniaceae, but the greatest number occur among the Cyatheaceae and Polypodiaceae. The dictyostelic condition has been derived from the siphonostelic by the overlapping of leaf gaps, so that several or many separate vascular strands are seen in a cross section of the stem. In complex dictyosteles the vascular cylinder consists of a tubular network.

A transverse section of the rhizome of *Polypodium* shows a number of small, widely separated vascular strands arranged in a circle. The rhizome of *Pteridium*, which is dorsiventral, consists of two series of strands—a circle of small peripheral ones enclosing two large central strands, or sometimes more than two as a result of branching (Fig. 238). The dorsal bundle is band-like and larger than the other peripheral ones.

The bundles are amphicribral with mesarch xylem (Fig. 239). Each is surrounded by an endodermis that encloses a continuous pericycle usually comprising only a single layer of cells. The ground tissue of the rhizome consists of parenchyma surrounded by an outer zone of thick-walled cells. In the central region are two transverse bands of sclerenchyma, one occurring above and one below the medullary strands. The lower band is larger than the upper one and slightly curved.

Sorus. In most of the Filicales the sporangia are borne on the abaxial surface of ordinary foliage leaves. In the Schizaeaceae the sporangia are solitary, but in the other families they occur in groups called *sori*. Generally the sori are arranged on either side of the midrib, but in many genera they are marginal or nearly so (Fig. 240). Ordinarily the leaf segments that bear the sporangia are unmodified. Often, however, a marked differentiation exists between sterile and fertile leaflets, the latter being conspicuously contracted. This condition prevails in *Osmunda*, the Schizaeaceae, *Onoclea*, *Blechnum*, etc. The same leaf may produce both sterile and fertile leaflets, or the entire leaf may be made up of either one kind or the other.

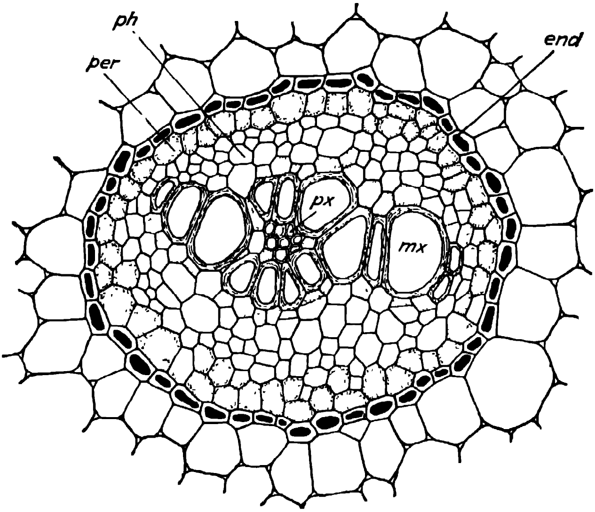

FIG. 239 Cross section of a vascular bundle from the rhizome of *Pteridium aquilinum*, ×200; *end*, endodermis, *per*, pericycle; *ph*, phloem; *px*, protoxylem; *mx*, metaxylem

Some ferns have naked sori, but usually each sorus is covered by a flap-like membrane called the *indusium* (Fig. 240). Although absent in the Osmundaceae and Gleicheniaceae, an indusium is present in the Schizaeaceae, Hymenophyllaceae, Dicksoniaceae, Cyatheaceae (except *Alsophila*), and in most of the Polypodiaceae (*Polypodium* being a notable exception) Generally the indusium represents a special outgrowth of the leaf, but i may be formed by the inrolled leaf margin. Such a "false indusium" is present in the Schizaeaceae, Hymenophyllaceae, Dicksoniaceae, and in such well-known genera of Polypodiaceae as *Pteris*, *Pteridium*, *Adiantum*, *Pellaea*, *Cheilanthes*, and *Notholaena* (Fig. 240*B*, *D*). This condition may be regarded as primitive. In a number of true ferns the sori lose their individuality by a spreading of the sporangia over the leaf surface or along the leaf margin. Such "confluent sori" are seen in *Pityrogramma*, *Elaphoglossum*, *Pteris*, and *Pteridium*.

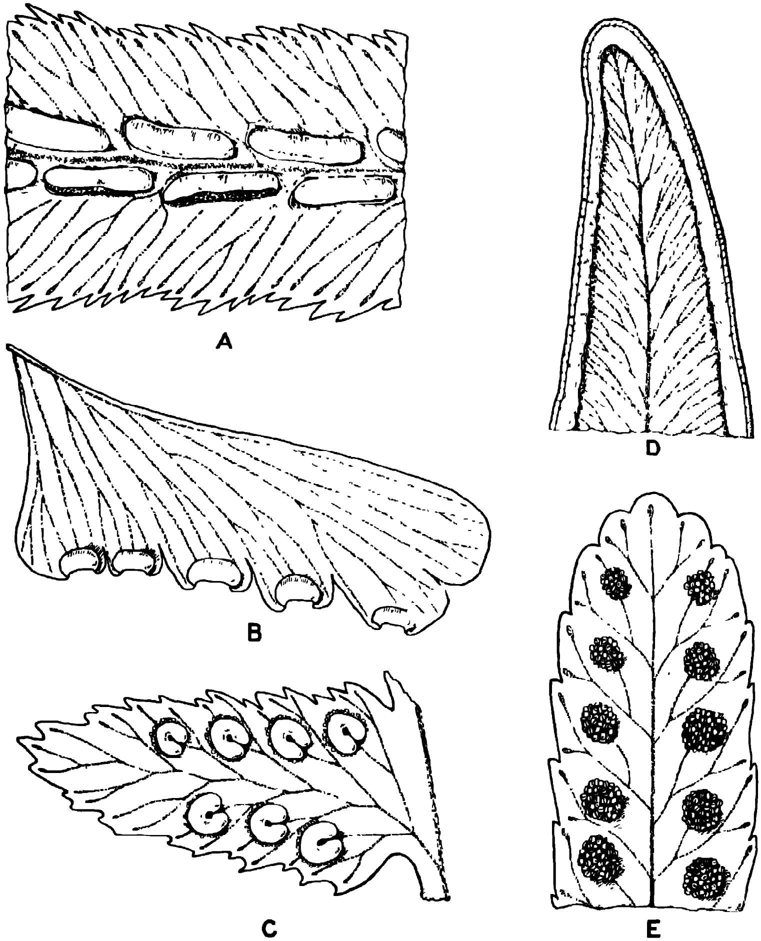

FIG. 240. Portion of the leaflets of five common ferns, illustrating differences in sori and indusia, ×4. *A*, *Woodwardia*; *B*, *Adiantum*; *C*, *Dryopteris*; *D*, *Pteridium*; *E*, *Polypodium*. In *B* and *D* a false indusium is seen, while in *E* there is no indusium.

With respect to the order of appearance of the sporangia within the sorus, three conditions are recognized, as follows: (1) The *simple sorus*, where all the sporangia arise at the same time and therefore are all of the same age, is found among the most primitive families, *viz.*, Osmundaceae, Schizaeaceae, and Gleicheniaceae. (2) The *gradate sorus*, in which the sporangia arise in basipetal succession on an elongating receptacle, occurs in the Hymenophyllaceae, Dicksoniaceae, and Cyatheaceae. (3) The *mixed sorus*, where sporangia of different ages are intermingled in the same sorus and show no developmental sequence, is the most advanced type. It is characteristic of all the Polypodiaceae except *Woodsia* and *Onoclea*, which are gradate.

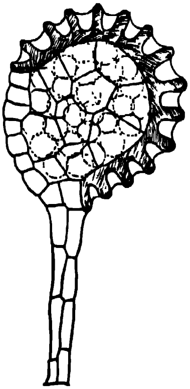
FIG. 241. Mature sporangium of one of the Polypodiaceae, showing the incomplete vertical annulus, ×150.

Sporangium. The sporangium in the Polypodiaceae is slightly flattened and has a long, slender stalk (Fig. 241). It also has a rather long stalk in the Dicksoniaceae and Cyatheaceae, but in the lower families it has a short, stout stalk or none. In all the Filicales the sporangium wall consists of a single layer of cells. A special feature is the presence of an *annulus*, a group or, more commonly, a ring of specialized cells that brings about the dehiscence of the sporangium. Its cells have all but their outer walls thickened. Drying causes a contraction of the thickened band, resulting in a state of tension that finally ruptures the sporangium wall. As the annulus bends backward, the spore mass is exposed. Then, suddenly, the annulus springs to its original position, hurling the spores into the air.

The Osmundaceae have a rudimentary annulus (Fig. 242). In both this family and the Schizaeaceae the annulus is apical, while in the Gleicheniaceae it is equatorial. Dehiscence in all three families is longitudinal. In the Hymenophyllaceae, Dicksoniaceae, and Cyatheaceae the annulus is oblique and the dehiscence is obliquely lateral. In the Polypodiaceae the annulus is vertical, extending only about two-thirds of the way around the sporangium (Fig. 241). Dehiscence is transverse.

The Filicales resemble the Ophioglossales and Marattiales in being homosporous, but differ in that they are *leptosporangiate*. This means that the sporogenous tissue is developed from the outer segment arising from the first periclinal division of the initial, rather than from the inner segment, as among eusporangiate pteridophytes. The sporangium initial consists of a single superficial or marginal cell that becomes papillate. A periclinal division separates an inner cell from an outer cell, and then three oblique walls appear in the latter in such a way that a tetrahedral apical cell is formed. This cuts off a variable number of segments that form a short stalk (Fig. 243*A*). The sporangium now enlarges above and, by means of a periclinal division, an outer *cap cell* is separated from an inner *primary sporogenous cell* (Fig. 243*B*). The sporangium wall is developed by subsequent anticlinal divisions from the cap cell and the three uppermost stalk cells (Fig. 243*C*). In all the Filicales the sporangium wall remains one layer of cells thick.

A unique feature is introduced by the formation of the tapetum from the primary sporogenous cell rather than from the wall tissue. The tapetum arises from four cells, one of which is cut off each of the four faces of the primary sporogenous cell (Fig. 243*D*, *E*). The tapetum may remain single-layered, but in nearly all the Filicales its cells divide periclinally to form two layers (Fig. 243*F*, *G*). The innermost cell of the sporangium meanwhile undergoes division to form the spore mother cells (Fig. 243*F*–*H*). When these round off, the tapetum disorganizes and forms a plasmodium that later surrounds them. The number of spores formed in each sporangium exhibits considerable variation, but is relatively high (up to 512) in the lower families and relatively low (commonly 64 or less) in the advanced families. This tendency to reduce the spore output is a significant feature of Filicinean evolution.

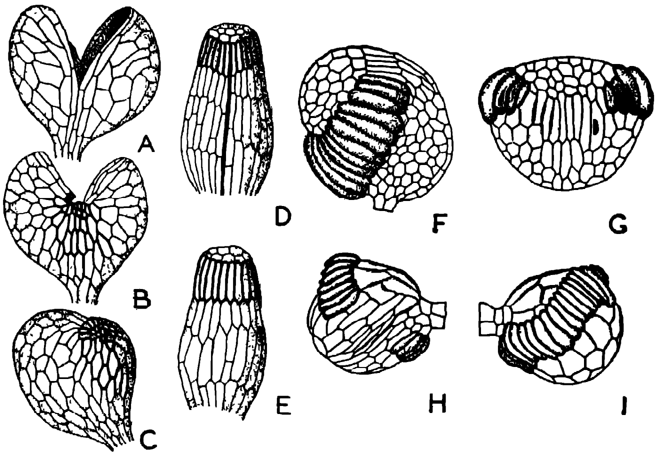

FIG. 242 Sporangia of some leptosporangiate ferns. *A*, *B*, *C*, *Osmunda regalis*, with rudimentary annulus; *D* and *E*, *Anemia phyllitidis*, with apical annulus; *F* and *G*, *Gleichenia circinata*, with equatorial annulus; *H* and *I*, *Hymenophyllum dilatum*, with oblique annulus. (*After Wettstein.*)

Gametophyte. The typical gametophyte of the Filicales is entirely aerial and consists of a flat, green, heart-shaped thallus usually about 6 mm. in diameter (Fig. 244). Numerous unicellular rhizoids grow from its ventral surface into the soil. There is no endophytic fungus, except in the Gleicheniaceae and sometimes in the Schizaeaceae and Hymenophyllaceae. In *Hymenophyllum* the gametophyte is an irregularly branched ribbon, while in *Trichomanes* and *Schizaea* it is filamentous and branched, resembling a moss protonema.

The germinating spore gives rise to a short green filament and a rhizoid. Soon an apical cell with two cutting faces arises and a flat thallus develops. Then an apical cell with three cutting faces is formed and the median portion of the prothallium becomes slightly thickened, the wings remaining one-layered. Eventually a group of initials is formed in the apical notch, replacing the apical cell.

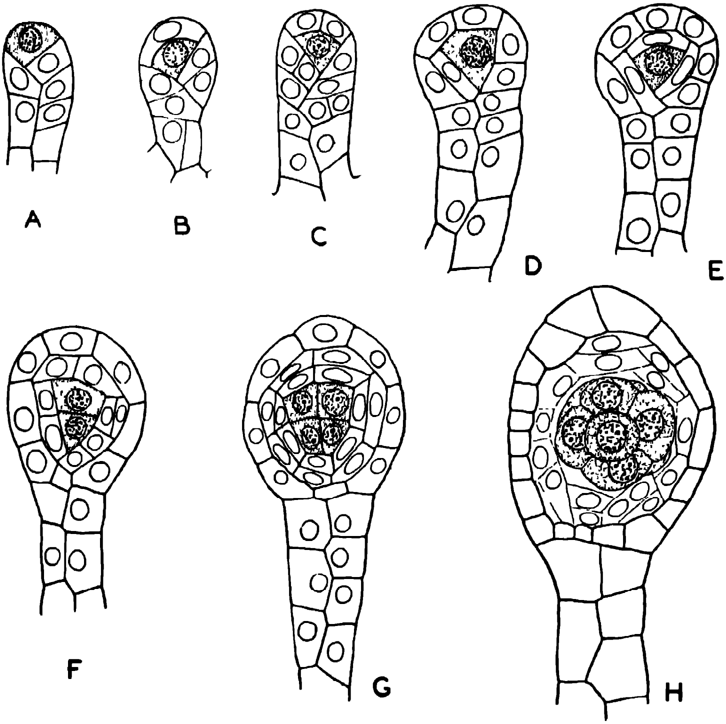

FIG. 243. Development of the sporangium of *Cyrtomium falcatum* (Polypodiaceae), ×400. *A*, young stage, showing tetrahedral apical cell cutting off segments to form a stalk; *B*, formation of cap cell and primary sporogenous cell; *C*, anticlinal division of cap cell; *D*, formation of first tapetal cell from primary sporogenous cell; *E*, completion of tapetum; *F* and *G*, later stages, the tapetum becoming two-layered; *H*, breaking down of tapetum and rounding off of spore mother cells.

In most of the Filicales the prothallium is monoecious, the sex organs arising from the ventral surface. The antheridia appear at a very early stage, often when the prothallium is still filamentous, and continue to be produced for a long time. The first antheridia are often marginal as well as ventral in position. Later they become irregularly scattered over the entire ventral surface. The antheridia are not embedded in the prothallium but project beyond its surface.

The antheridia of the Filicales differ greatly in development from those of the lower pteridophytes (Fig. 245). The initial is superficial and papillate. The first wall is transverse, the antheridium developing from the outer cell. This then undergoes a second transverse division, cutting off a *basal ring cell.* Due to increasing turgidity of the upper cell, the wall formed, called the *funnel wall,* becomes concave and approaches the first wall, finally touching it (Fig. 245*A*). Next a *dome wall* appears, delimiting an outer cell from a central cell (Fig. 245*B*). The dome wall is hemispherical and nearly concentric with the outer surface of the antheridium. The appearance of a second funnel wall in the outer cell results in the formation of another ring cell and a cap cell, thus completing the sterile jacket (Fig. 245*C* *E*). The output of sperms in the higher families is commonly 32. As in the other ferns, the sperms are large, coiled, and multiciliate (Fig. 245*F*).

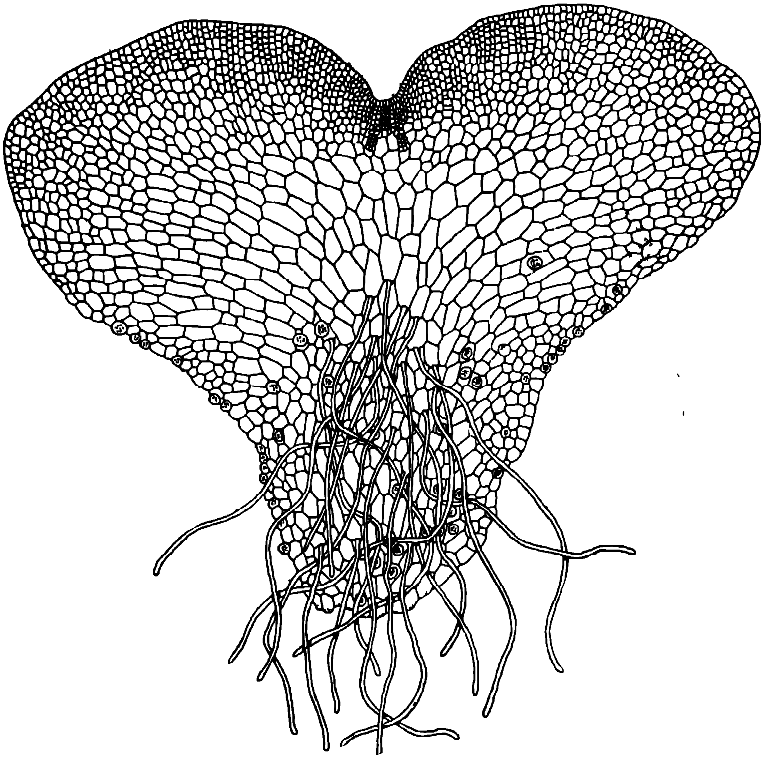

Fig. 244. Ventral view of a fern prothallium (Polypodiaceae), showing rhizoids and numerous antheridia in the older portion and three archegonia near the growing notch, ×35.

The archegonia appear late in the development of the gametophyte, thus occurring in the median portion near the growing notch (Fig. 244).

The initial is superficial but remains embedded. It divides transversely, the outer segment being the *primary neck cell* and the inner one dividing again to form the *central cell* and *basal cell* (Fig. 246*A*, *B*). The central cell gives rise to the axial row, which consists of a single binucleate *neck canal cell*, a small *ventral canal cell*, and the *egg* (Fig. 246*C*–*E*). In the Osmundaceae and Gleicheniaceae the neck canal nuclei may be separated by a wall. The venter of the mature archegonium is embedded in the prothallium, but the neck, which usually curves slightly backward, projects beyond the surface (Fig. 246*F*). The neck consists of four vertical rows of cells.

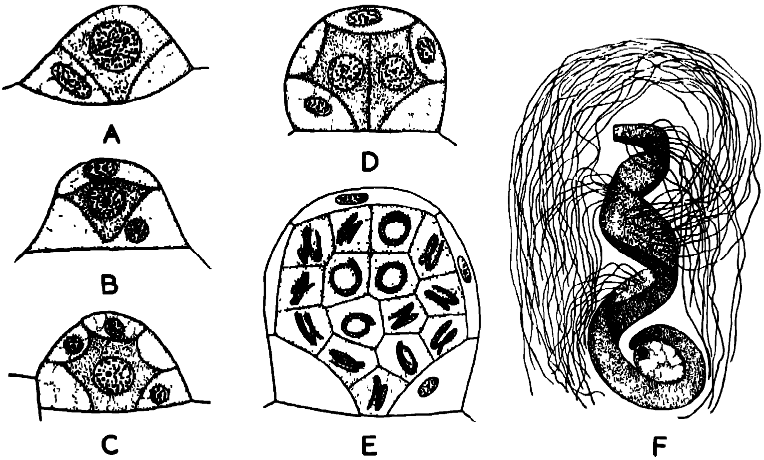

Fig. 245. Stages in development of the antheridium of *Nephrolepis* (*A to E*), ×700, and a sperm of *Dryopteris* (*F*), more highly magnified. *A*, cutting off a basal ring cell by funnel wall; *B*, appearance of dome wall, delimiting of outer cell from central cell; *C*, formation of second funnel wall; *D*, first division of central cell; *E*, mature antheridium with sperms forming in spermatogenous cells (*A to E*, *after Gilbert M. Smith; F*, *after Yamanouchi*)

Embryo. The Filicales are characterized by a striking regularity in the early divisions of the embryo. The first division of the fertilized egg is not transverse but vertical, *i.e.*, parallel with the long axis of the archegonium (Fig. 247*A*). By a division of each daughter cell at right angles to the plane of the first division, quadrants are formed (Fig. 247*B*). Of the two inner cells, the anterior one gives rise to the stem and the posterior one to the foot. Of the two outer cells (those nearer the neck of the archegonium), the anterior one forms the first leaf and the posterior one the primary root. Thus the arrangement of the quadrants differs conspicuously from that found among the eusporangiate ferns. The subsequent divisions are at first regular, resulting in a globular embryo in which the four primary organs may be easily distinguished (Fig. 247*C*). Later growth, however, is irregular, the leaf and root developing more rapidly and soon breaking through the calyptra (Fig. 247*D*).

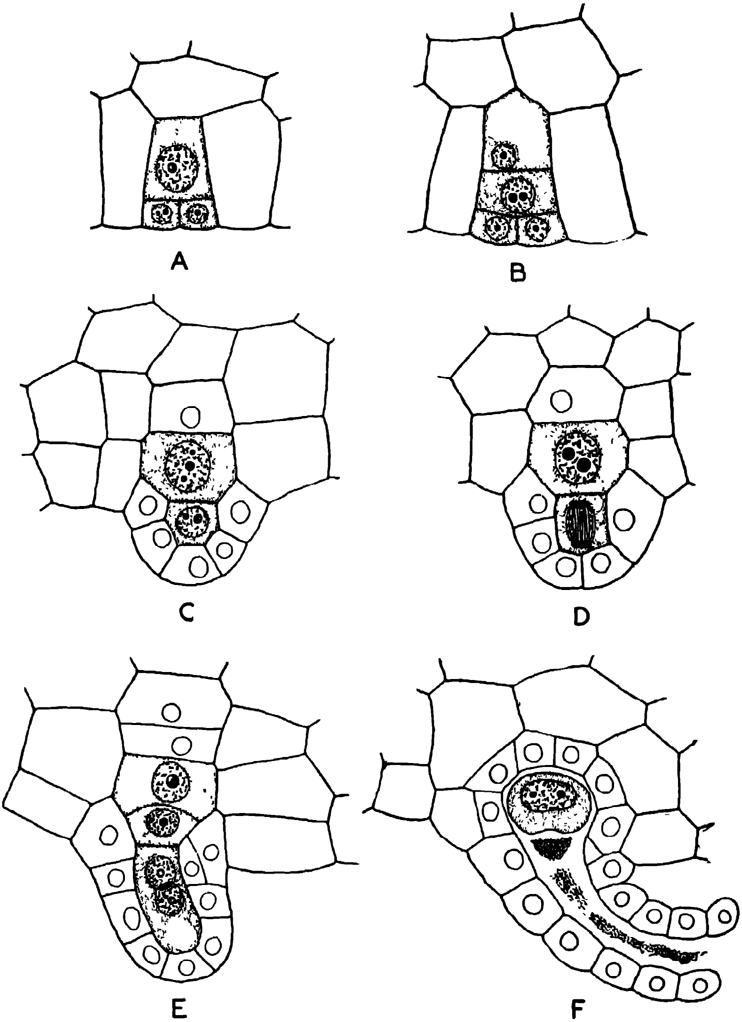

FIG. 246. Development of the archegonium of *Dryopteris*, ×350. *A*, division of archegonium initial into an inner and outer cell, the latter having again divided anticlinally to form two neck cells; *B*, formation of central cell and basal cell; *C*, division of central cell into ventral cell and neck canal cell; *D*, division of neck canal cell nucleus; *E*, nearly mature archegonium with egg, ventral canal cell, and binucleate neck canal cell; *F*, archegonium with egg ready for fertilization.

Summary. The Filicales are homosporous and leptosporangiate. The sporangia are borne on the abaxial side of the leaves and are not in synangia. The sporangium wall, one layer of cells thick, has an annulus. The vernation is circinate. The gametophyte is flat, green, and thin (sometimes filamentous); with few exceptions it is without an endophytic fungus. The development of the antheridium is characteristic. The inner portion of the embryo forms the stem and foot, the outer portion the leaf and root. The Filicales are a highly organized group. Their principal advance over the eusporangiate ferns lies in the development of their spore-producing structures.

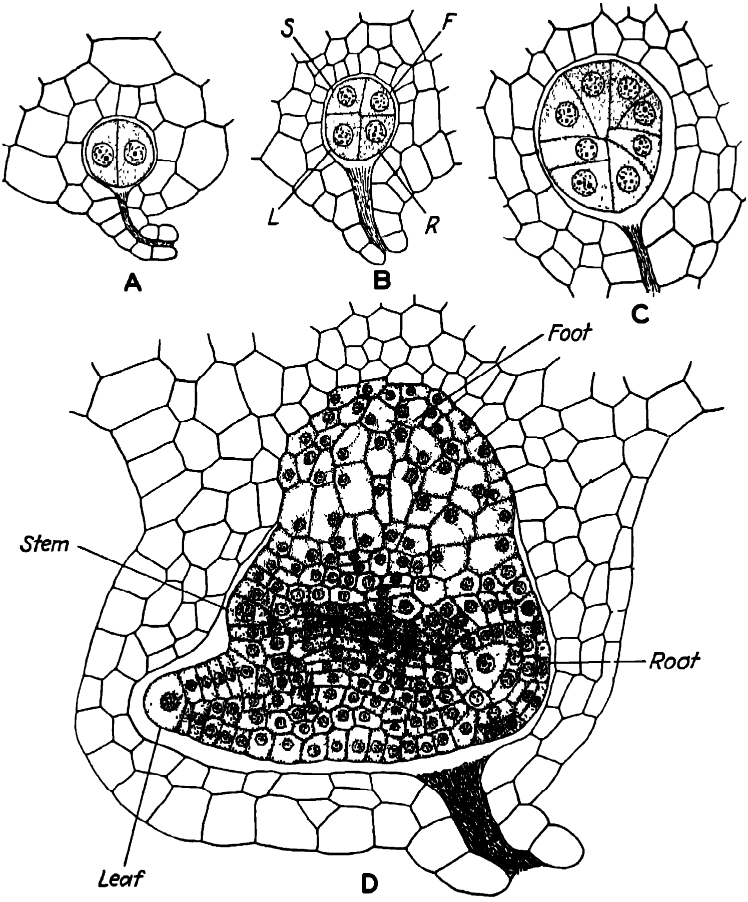

FIG 247. Stages in development of the embryo of a polypodiaceous fern, ×225. *A*, two-celled stage; *B*, four-celled stage; *C*, slightly later stage; *D*, embryo showing differentiation of organs.

5. Hydropteridales

The Hydropteridales include 2 families, 5 genera, and nearly 90 species. The two families are probably of separate origin and their inclusion in the same order is largely a matter of convenience. Both are more advanced than any of the families of Filicales, however, and in the same ways. All these plants live in water or in wet places and are appropriately called "water ferns." They constitute the most highly developed group of modern pteridophytes.

1. MARSILEACEAE

To the Marsileaceae belong 3 genera. *Marsilea*, with 65 species, and *Pilularia*, with 6 species, are widely distributed, while *Regnellidium*, with a single species, is confined to southern Brazil. They live on muddy flats or submerged in water, rooting in the mud.

FIG. 248. *Marsilea vestita* View of plants growing in swampy ground.

Sporophyte. In all three genera the stem is a slender, creeping, branched rhizome that produces erect leaves but no upright shoots. The leaves are arranged alternately in two rows along the upper side of the rhizome, while along the lower side roots are borne at the nodes. Each leaf of *Marsilea* has a long petiole and four terminal leaflets (Fig. 248). *Regnellidium* has two leaflets, while in *Pilularia* leaflets are wanting, the whole leaf consisting merely of a petiole. As in the Filicales, the leaves exhibit circinate vernation and dichotomous venation. The stem develops from a tetrahedral apical cell that cuts off three longitudinal rows of segments. The leaves arise from the two dorsal rows, the roots from the ventral row. The rhizome of *Marsilea* is an amphiphloic siphonostele without secondary thickening (Fig. 249). The rhizome of *Pilularia* is similar except that the vascular tissues are reduced.

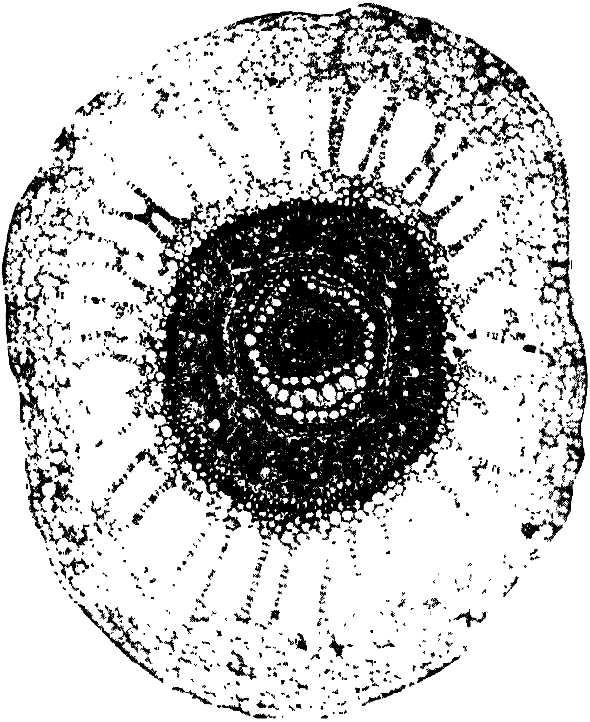

FIG. 249. Cross section of the rhizome of *Marsilea quadrifolia*, an amphiphloic siphonostele, X 50.

Sporocarp. The sporangia of the Marsileaceae are borne in special structures, called *sporocarps*, which occur on long or short stalks arising adaxially from the petiole of the leaf. They are usually borne singly, but in some species of *Marsilea* several or even many may be borne together. The sporocarp is a specialized leaf segment enclosing a group of sori. In *Marsilea* it is an ovoid or bean-shaped structure with a hard outer covering (Fig. 251). It contains 14 to 20 sori. In *Pilularia* the sporocarp is spherical and contains 2 to 4 sori. In both genera the sori are arranged in two rows. Each is surrounded by an indusium and contains both microsporangia and megasporangia. The sporangium wall is only one layer of cells in thickness, as in the Filicales, but is without an annulus.

The sporangia are leptosporangiate in development. Four cavities appear in the young sporocarp of *Marsilea* and from the layer of cells lining them the sporangia arise, each sorus coming from a single marginal cell (Fig. 250*A*). The sporangia appear in basipetal succession on an elongating receptacle, the sorus thus being gradate, as in certain families of the Filicales (see page 286). The tapetum, cut off from the sporogenous tissue, becomes two-layered (Fig. 250*B*). In both kinds of sporangia 32 or 64 young spores are formed. In the microsporangia all of these mature, but in the megasporangium only one spore matures, the others degenerating (Fig. 250*C*, *D*). The functional megaspore greatly enlarges

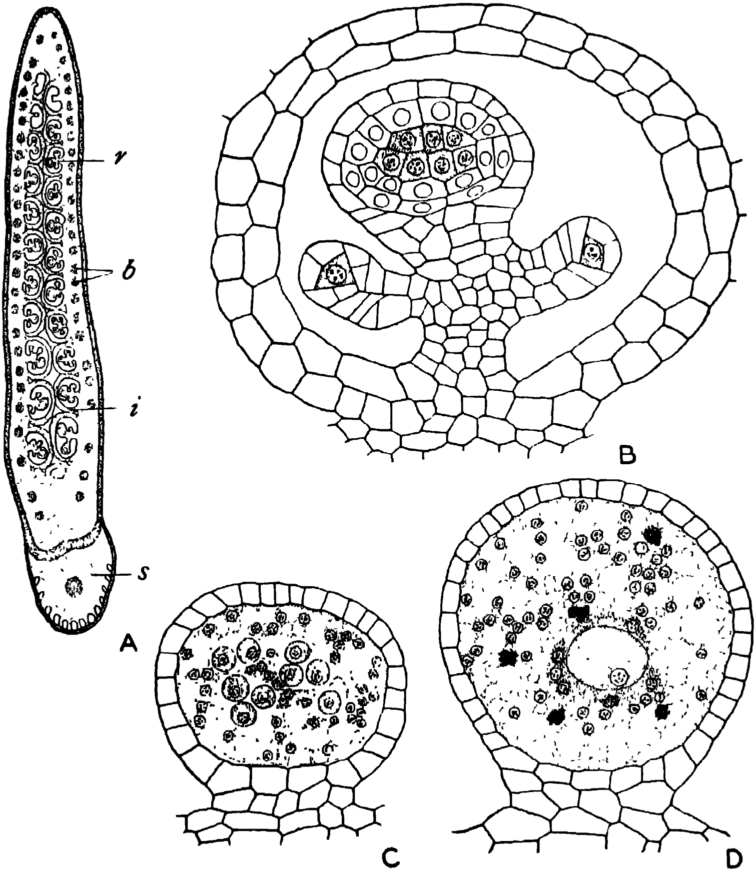

FIG. 250. Sporangia of *Marsilea quadrifolia*. *A*, horizontal section through a young sporocarp, showing early development of two rows of sori, ×25; *B*, longitudinal section through a young sorus and investing indusium, showing a developing megasporangium with sporogenous tissue and tapetum, and two younger microsporangia below, each with a primary sporogenous cell, ×400; *C*, megasporangium with young megaspores and tapetal plasmodium, ×300; *D*, megasporangium with enlarging functional megaspore, abortive megaspores, and tapetal plasmodium, ×300; *r*, receptacle; *b*, vascular bundles; *i*, indusium; *s*, stalk of sporocarp.

and develops a very thick cell wall, as in the other heterosporous pteridophytes. In both kinds of sporangia the tapetum breaks down to form a multinucleate plasmodium that surrounds and nourishes the young spores.

The sporocarp of *Marsilea* is remarkable on account of its longevity, some specimens having been known to have retained their viability for 50 years. If placed in water after the hard outer covering has been cracked, germination is unusually prompt. Within an hour a mucilaginous ring appears to which the sori are attached, each sorus being enclosed by its own indusium (Fig. 251). The spores germinate at once and the gametophytes develop with startling rapidity.

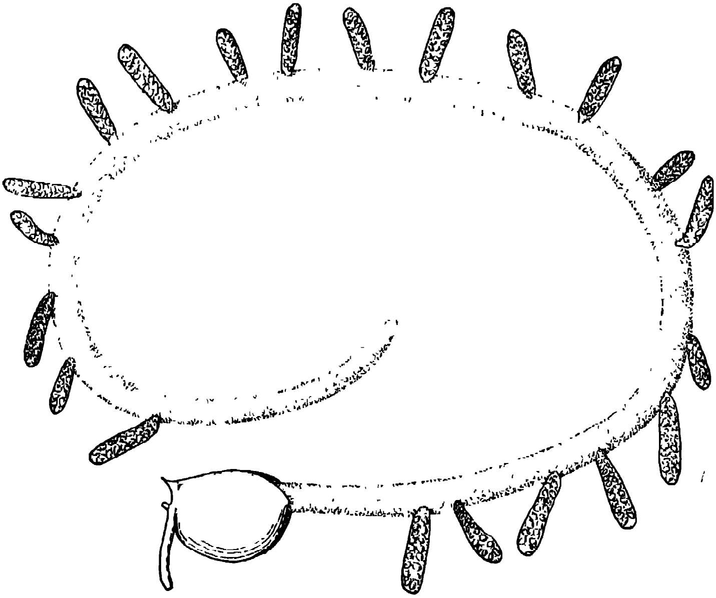

FIG 251. Germination of the sporocarp of *Marsilea vestita*, twice natural size. Extrusion of mucilaginous ring to which the sori are attached.

Gametophytes. The male gametophyte of *Marsilea* reaches maturity within 10 to 20 hours after the microspore germinates. It does not emerge from the spore, but develops inside, as in *Selaginella* and *Isoetes*. After a prothallial cell is cut off, the rest of the spore divides in half, each half becoming an antheridium (Fig. 252*A*–*C*). Additional divisions result in the formation of two primary spermatogenous cells surrounded by a sterile jacket (Fig. 252*D*–*F*). Each of the primary spermatogenous cells gives rise to a group of 16 sperms (Fig. 252*G*–*I*). The sperms of *Marsilea* are corkscrew-like and multiciliate (Fig. 252*J*).

The female gametophyte of *Marsilea* is peculiar in that no internal tissue is developed and only one archegonium is formed. At the apex of the megaspore, where the wall is relatively thin, there is a papilla filled with dense cytoplasm in which the nucleus lies (Fig. 253*A*). When the spore germinates, the nucleus divides and a small cell is cut off by a transverse wall (Fig. 253*B*). The rest of the gametophyte acts as a food reservoir. The small cell is the archegonium initial, the larger one the nutritive cell. As development proceeds, the archegonium breaks through the megaspore wall. The mature archegonium consists of a large egg, a small ventral canal cell, a small neck canal cell, and a sterile jacket (Fig. 253*D*). The neck is short, consisting of only two tiers of four cells each. Mucilage above the archegonium forms a deep funnel into which the sperms collect.

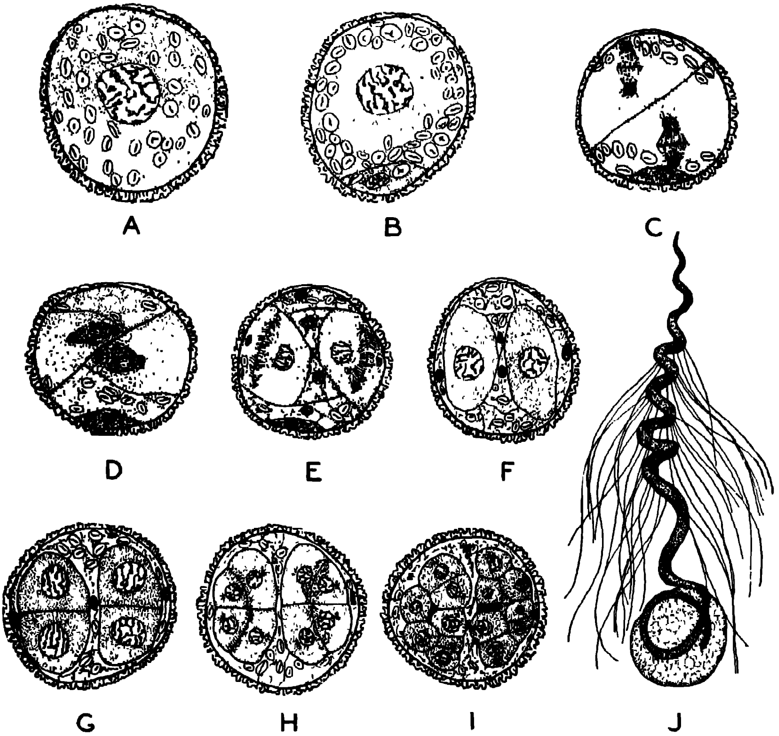

Fig. 252. Male gametophyte of *Marsilea quadrifolia*. *A*, microspore with starch grains in cytoplasm; *B*, prothallial cell cut off; *C*, microspore divided into two antheridium initials, in each of which a jacket cell is being formed; *D* and *E*, additional jacket cells being cut off, *F*, two primary spermatogenous cells enlarging; *G*, *H*, *I*, stages showing increase in spermatogenous cells to sixteen in each of the two antheridia; *J*, mature sperm, ×1,200; other stages, ×350. (*After Sharp.*)

Embryo. In the development of the embryo, the first wall is vertical, as in the Filicales, and then a quadrant stage appears (Fig. 253*E*). The

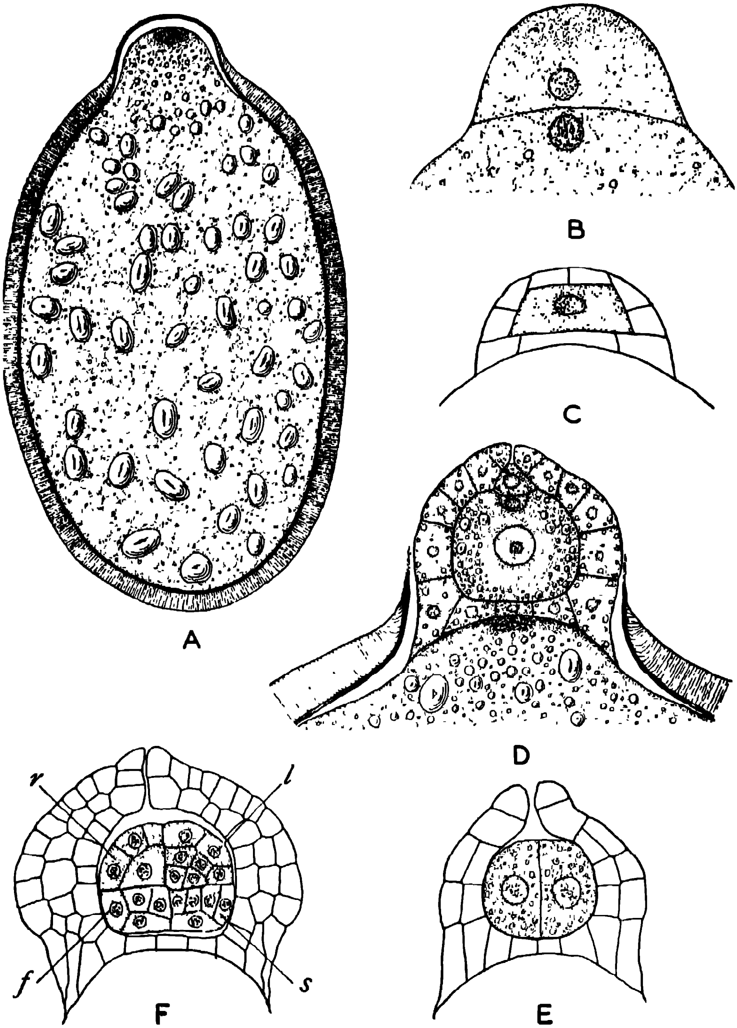

FIG. 253 Female gametophyte of *Marsilea quadrifolia*. *A*, longitudinal section of megaspore; *B*, archegonium initial cut off at apex of spore; *C*, young archegonium with central cell surrounded by neck cells and sterile jacket; *D*, mature archegonium, showing large egg, small ventral canal cell, and neck canal cell; *E*, two-celled embryo; *F*, embryo, enclosed by calyptra, showing differentiation into foot (*f*), root (*r*), leaf (*l*), and stem (*s*); *A*, ×100, *B* to *F*, ×250.

arrangement of the segments is such that the two outer segments (those nearer the neck of the archegonium) give rise to the leaf and root, the two inner ones to the stem and foot, the leaf and stem developing from segments on the same side (Fig. 253*F*). With respect to the arrangement of the primary organs, the embryo of the Marsileaceae is similar to that of the Filicales.

2. SALVINIACEAE

To the Salviniaceae belong 2 genera of widespread occurrence, *Salvinia*, with 11 species, and *Azolla*, with 4 species. Both are small plants that float on the surface of quiet water. Their fossil history does not extend beyond the Tertiary.

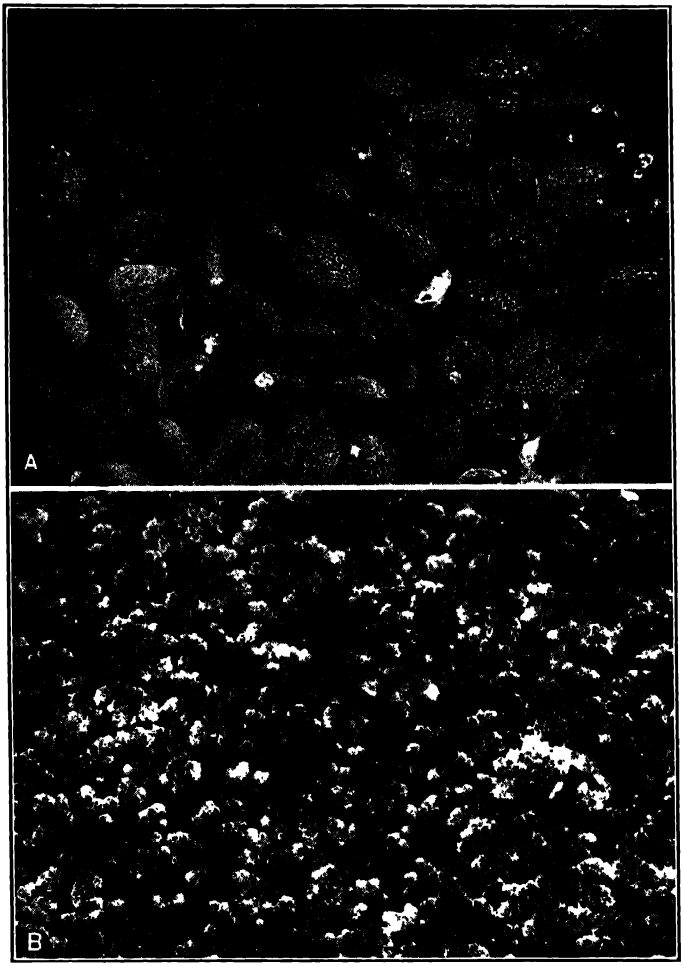

FIG. 254. Floating plants of *Salvinia rotundifolia* (*A*), natural size, and of *Azolla filiculoides* (*B*), twice natural size.

Sporophyte. *Salvinia* has a slender, slightly branched stem bearing two kinds of leaves. The dorsal leaves are in four rows (Fig. 254*A*). They are 12 to 18 mm. long, entire, oval or oblong, flat, and overlapping. The ventral leaves, which occur in two rows, hang down into the water and look like roots, being much dissected into filiform divisions. The ventral leaves are probably absorptive in function, true roots being wanting. *Azolla* has pinnately branched stems covered with minute, crowded, overlapping leaves alternately arranged in two dorsal rows (Fig. 254*B*). Each leaf has two lobes, the upper lobe floating and the lower one submerged. The upper lobe contains cavities in which colonies of *Anabaena* live. Long, slender rootlets arise from the lower side of the stem.

In both genera the leaves are folded in the bud, not circinate as in the Marsileaceae and Filicales. Each leaf has a single vascular bundle. The stem develops by means of an apical cell with two cutting faces. The vascular tissues are greatly reduced. The stem of *Salvinia* appears to be an ectophloic siphonostele, that of *Azolla* an amphicribral protostele.

Sporocarps. The sporocarps of the Salviniaceae are globular and thin-walled, two or three occurring on a common stalk. In *Salvinia* they are borne in groups at the base of the ventral leaves, arising as outgrowths from them. In *Azolla* they are borne on lateral branches, chiefly in pairs, on the lower lobes of the first leaves to appear. In both genera the sporocarps consist of an indusium enclosing a single sorus. The indusium becomes hard at maturity, forming a nut-like structure.

The sporocarps are of two kinds, both occurring on the same plant. One contains only microsporangia and the other only megasporangia. In *Salvinia* the two kinds of sporocarps are of the same size and contain many sporangia, but in *Azolla* the megasporocarps are much smaller than the microsporocarps and contain only one megasporangium. At first each sporocarp of *Azolla* contains a young megasporangium with several younger microsporangia at its base. Only one kind of sporangium continues its development, however, the other kind aborting (Fig. 255). In both genera the microsporangia are borne on long, slender stalks arising from a basal receptacle, while the megasporangia are short-stalked or nearly sessile (Figs. 255 and 256*A*). As in the Marsileaceae, the sorus is gradate. The sporangium wall is only one layer of cells thick and no annulus is formed.

As in the Marsileaceae and Filicales, the development of the sporangia is leptosporangiate (Figs. 255*A* and 256*B*). In the microsporangium of both *Salvinia* and *Azolla* 16 spore mother cells are formed and all of these give rise to tetrads, resulting in the formation of 64 microspores. In the megasporangium of both genera, however, only 8 spore mother cells are formed. These give rise to 32 megaspores, but only one of these matures, the rest degenerating (Fig. 256*D*). The functional megaspore enlarges until it finally completely fills the sporangium. It becomes very thick-walled. In both genera the tapetum, which is cut off from the sporogenous tissue and consists of a single layer of cells, breaks down before the spores are ripe, forming a plasmodial matrix around them (Figs. 255*B* and 256*C*, *D*). Eventually this hardens.

In the microsporangium of *Azolla* four to eight masses, called *massulae*, are organized from the tapetal plasmodium and within these the microspores are embedded. The massulae of some species of *Azolla* produce hair-like appendages (*glochidia*) with sagittate tips (Fig. 257*A*). They escape from the microsporangia and are carried to the megaspores, to which they become fastened by means of the glochidia. The microspores germinate within the massulae. In *Salvinia* they germinate while still within the microsporangia. The megaspores remain inside the megasporangia, which break away and, in *Salvinia*, float on the surface of the water.

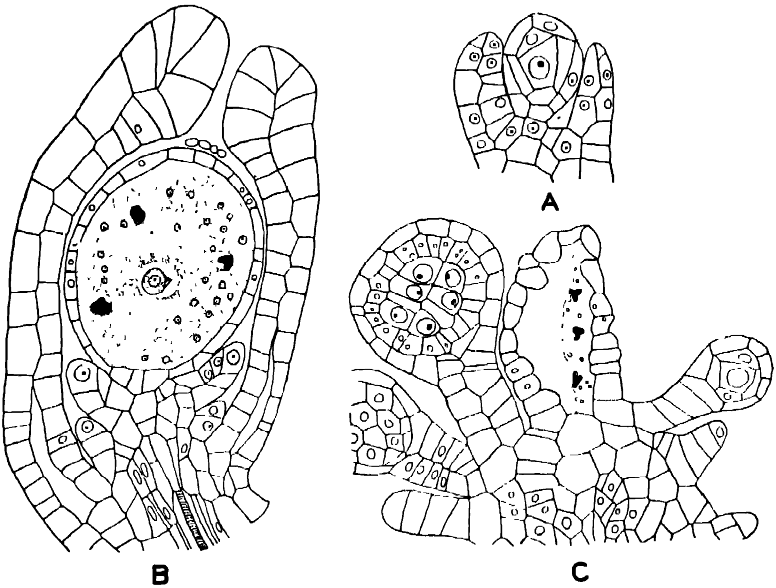

FIG 255. Sporangia of *Azolla caroliniana*. *A*, young sporocarp, showing a young megasporangium and the developing indusium, *B*, megasporocarp, showing the terminal megasporangium with one functional and three abortive megaspores, and undeveloped microsporangia below, *C*, microsporocarp with developing microsporangia and an abortive megasporangium. (*After Pfeiffer*)

Gametophytes. The male gametophyte of the Salviniaceae is peculiar in that the microspore produces a papillate outgrowth that forms one or two external antheridia, the internal portion functioning as a large nutritive cell (Fig. 257*B*). In both genera a small prothallial cell is cut off from the nutritive cell. In *Salvinia*, where there are two antheridia, each is enclosed by a sterile jacket and each produces four sperms. In *Azolla* there is only one antheridium and it produces eight sperms (Fig. 257*C*). The sperms are coiled and multiciliate.

In the formation of the female gametophyte, the nucleus of the megaspore divides near the apical end and a small lenticular cell is cut off. The larger cell later undergoes free-nuclear division, but no walls are formed and the cell becomes a food reservoir. The smaller cell gives rise to a tissue that breaks through the heavy megaspore wall and produces several archegonia (Fig. 257*D*). This tissue turns green and becomes rather extensive in *Salvinia*, but in *Azolla* is smaller and has little or no chlorophyll. The archegonia resemble those of *Marsilea,* except that the single neck canal cell is usually binucleate.

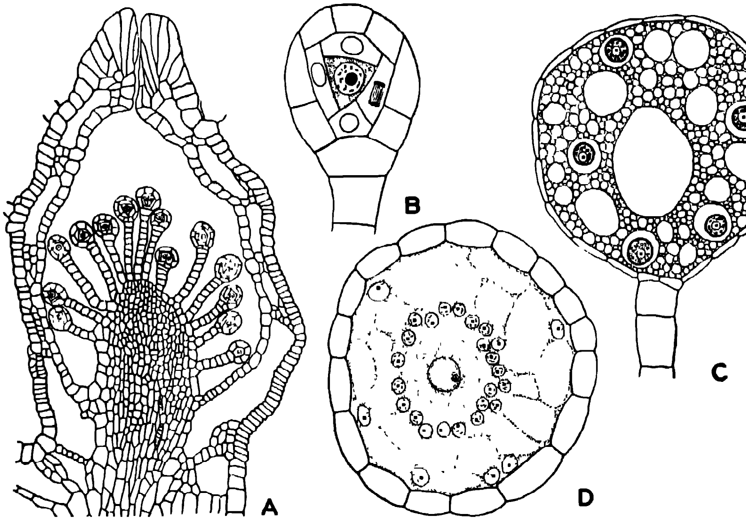

FIG. 256. Sporangia of *Salvinia rotundifolia* *A*, longitudinal section through a young microsporocarp, ×100; *B*, young microsporangium, showing primary sporogenous cell surrounded by tapetum, ×600; *C*, older microsporangium, showing spores embedded in hardened tapetal plasmodium, ×160; *D*, developing megasporangium, showing young functional megaspore surrounded by tapetal nuclei, the nonfunctional megaspores near the wall, ×280

Embryo. In both genera the fertilized egg, by means of two divisions at right angles to each other, gives rise to quadrants, but the first wall is longitudinal in *Salvinia* and transverse in *Azolla*. The relation of the four primary organs to one another is the same as in the other leptosporangiate ferns.

Summary. The Hydropteridales are heterosporous and leptosporangiate. The sporangia are borne in sporocarps representing either a modified leaf segment (Marsileaceae) or a modified indusium (Salviniaceae). Both microsporangia and megasporangia occur in the same sporocarp (Marsileaceae) or in separate sporocarps (Salviniaceae). The sporangium wall is only one layer of cells thick and is without an annulus. The vernation is circinate (Marsileaceae) or folded (Salviniaceae). The gametophytes are greatly reduced, developing largely within the spore wall. The development of the embryo is essentially the same as in the Filicales. The Hydropteridales are a specialized aquatic group, the two families apparently having been derived independently from the Filicales.

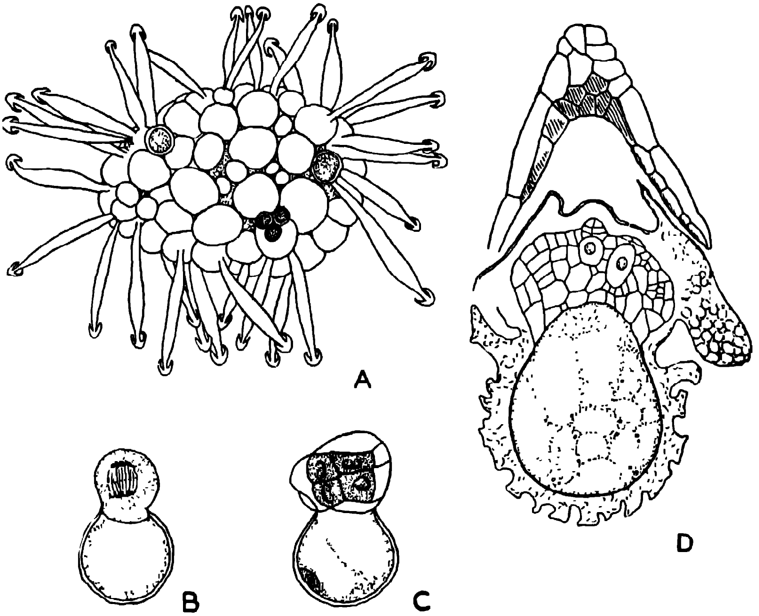

FIG. 257. *Azolla filiculoides.* *A*, massula with glochidia and enclosed microspores, ×250, *B*, germinating microspore, the antheridium initial dividing, ×560; *C*, male gametophyte with small prothallial cell, large nutritive cell, and external antheridium, ×560; *D*, female gametophyte, showing the large nutritive cell and the extruded tissue bearing archegonia, ×65. (*After Campbell.*)

COMPARISON OF THE CLASSES OF PTERIDOPHYTES

The most important distinguishing characters of the four classes of pteridophytes are as follows:

Psilophytinae. Leaves small, simple, spiral, generally without veins, often wanting. Roots absent. Stem mostly an exarch protostele. Leaf gaps absent. Definite strobili not organized. Sporangia solitary, terminal; on elongated branches and unilocular or (in Psilotales) on greatly reduced branches and bilocular or trilocular; tapetum wanting. Homosporous. Prothallia (in Psilotales) tuberous, subterranean, not green. Sperms multiciliate. Embryo without a suspensor.

Lycopodiinae. Leaves simple, usually small and numerous, generally spiral, with a single vein. Stem mostly an exarch protostele. Leaf gaps absent. Definite strobili usually present. Sporangia borne on sporophylls, solitary, adaxial, unilocular; trabeculae sometimes present. Homosporous (in Lycopodiales) or heterosporous. Prothallia in homosporous forms tuberous, wholly or in part subterranean, and with chlorophyll only in the aerial portion. Sperms biciliate or (in Isoetales) multiciliate. Embryo with or (in Isoetales) without a suspensor.

Equisetinae. Leaves mostly small and simple, numerous, cyclic, with a single vein. Stems conspicuously jointed, longitudinally grooved. Stem an endarch siphonostele or (in Sphenophyllales) an exarch protostele. Leaf gaps absent. Strobili present. Sporangia generally borne in groups on sporangiophores, usually adaxial with reference to the sporophylls, which are frequently absent. Homosporous or heterosporous. Prothallia (in Equisetales) flat, aerial, green. Sperms multiciliate. Embryo without a suspensor.

Filicinae. Leaves mostly few, large, and divided, spiral, with numerous veins. Stem a protostele, siphonostele, or dictyostele; typically mesarch. Leaf gaps present. Strobili absent. Sporangia numerous and generally abaxial on modified or unmodified leaflets, commonly in sori. Homosporous or (in Hydropteridales) heterosporous. Prothallia in homosporous forms flat, green, and aerial or (in Ophioglossales) tuberous, subterranean, and not green. Sperms multiciliate. Embryo nearly always without a suspensor.

GENERAL CONCLUSIONS

All pteridophytes have archegonia and multicellular antheridia, although these organs are somewhat reduced as compared with those of bryophytes. Fertilization is still conditioned by the presence of water. All pteridophytes display a distinct alternation of generations, but advance far beyond the bryophytes in the possession of an independent sporophyte with a leafy stem, true roots, and a well-developed vascular system. The sporophyte is nourished by the gametophyte only during the early stages of its development.

Independent Sporophyte. In the evolution of the plant kingdom the first land plants to have established an independent sporophyte must necessarily have developed one with (1) a means of anchorage and of absorbing water directly from the soil and (2) a means of displaying green tissue to the light and air. In practically all existing pteridophytes the sporophyte carries on water absorption by roots and photosynthesis by leaves borne on a stem. Food manufacture has become primarily a function of the sporophyte, leaving fertilization as the main function of the gametophyte. This arrangement permits the sporophyte to grow upward into the air. A large plant displaying leaves to the light and air requires a constant supply of water as well as a means of mechanical support.

These demands are met, in the pteridophytes, mainly by the vascular system. Thus the sporophyte, in achieving independence, has developed roots, stems, and leaves, with a system of conducting and supporting tissues extending throughout the plant body.

Among existing pteridophytes the Psilotales are unique in having a sporophyte that shows little organization into vegetative organs. Their poorly developed leaves (without veins in *Psilotum*) and lack of roots, although probably related to a partially saprophytic existence, are to be regarded as primitive features, since they are shared with the extinct Psilophytales, a group which the Psilotales resemble in other respects as well.

The size of the leaves must be considered in relation to the size of the stem. From this standpoint, small simple leaves, without a petiole, are found in nearly all members of the three lower classes, while large leaves, with a petiole and with a blade that is almost always divided into leaflets, are characteristic of the ferns. Moreover, ferns are the only pteridophytes having leaf gaps, a feature setting them off in marked contrast to the lower classes and indicating a relationship to the seed plants, where leaf gaps are universally present. Except in the Equisetinae, where they are cyclic, the leaves of pteridophytes are fundamentally spiral in arrangement.

The leaves of the Psilophytinae, except those of *Tmesipteris*, are veinless, while those of the Lycopodiinae have a single unbranched vein. These groups are said to be *microphyllous* (small-leaved), for even the leaves of the Lepidodendrales and Isoetales, though larger than those of other lycopods, are narrow and have only one vein. The leaves of microphyllous pteridophytes probably represent emergences, or simple outgrowths from the stem. The Filicinae are *megaphyllous* (large-leaved) and their leaves have many branching veins. Such leaves apparently have evolved from a lateral branch system that has become flattened and limited in growth. Thus the leaves of lycopods and those of ferns have probably had a different origin and so are not homologous. Most of the Equisetinae have small simple leaves with a single vein, but some of the fossil members have larger leaves with leaflets and branching veins. This indicates that the group was originally megaphyllous, the small leaves having been derived from larger ones by reduction.

The Strobilus. A second contribution of the pteridophytes to the evolution of the plant kingdom has been the organization of a strobilus. Originally no distinction may have existed between sporophylls and foliage leaves, a condition found in the simpler species of *Lycopodium*. But gradually, as a result of "division of labor," sporophylls became less leaf-like and were organized to form a compact strobilus. Although not present in modern ferns, a strobilus is characteristic of nearly all the other groups of living pteridophytes, as well as of a number of extinct forms. Its appearance is important because it is a feature carried on into the spermatophytes.

In the Lycopodiinae and Filicinae the sporangia are borne in connection with some or all of the leaves. In the Lycopodiinae they are solitary and adaxial, in the Filicinae numerous and mainly abaxial. In the Psilophytinae the sporangia are terminal, either on the main stem (Psilophytales) or on a very short lateral branch (Psilotales). In the Equisetinae the sporangia are borne on sporangiophores. The sporangium of the pteridophytes is always epidermal in origin and may arise from a single cell or a small group of cells. In its development, all pteridophytes are eusporangiate except two orders of ferns, the Filicales and Hydropteridales, which are leptosporangiate. With the exception of the Psilotales, a tapetum is present in all living pteridophytes. In the Lycopodiinae the tapetum is persistent, but in the Equisetinae and Filicinae it soon breaks down.

Heterospory. The appearance of heterospory represents a third great forward step in evolution introduced by the pteridophytes. Among modern representatives it occurs only in *Selaginella*, *Isoetes*, and the five genera of the Marsileaceae and Salviniaceae. Heterospory was developed, however, in many extinct forms. It introduces into the life history two kinds of spores, two kinds of gametophytes, and a great reduction in the gametophyte generation. Heterospory, introduced by the pteridophytes, is an established feature of the spermatophytes. In fact, it makes seed formation possible.

The gametophytes of homosporous pteridophytes may be tuberous and subterranean, as in the Psilotales, Lycopodiales, and Ophioglossales, where the absence of chlorophyll is associated with a saprophytic mode of nutrition; or they may be flat, green, and aerial, as in the Equisetales, Marattiales, and Filicales. In practically all homosporous pteridophytes both kinds of sex organs are borne in comparatively large numbers on the same gametophyte. In the heterosporous forms, however, the gametophytes are always dioecious and reduced, both kinds developing largely or entirely within the spore wall. The male gametophyte produces only one or two prothallial cells and one or two antheridia. The female gametophyte usually has more vegetative tissue, but generally only one to several archegonia.

The gametophyte of the homosporous pteridophytes, with much vegetative tissue, must not only make its own food, but also enough for the embryo sporophyte that is dependent upon it. The development of such a gametophyte requires a considerable period of favorable external conditions. This handicap is largely avoided by the heterosporous pteridophytes. Their gametophytes are formed inside the spores that produce them and do not emerge except, in some cases, to a very slight extent. Each lives on food stored within the spore. The advantage of heterospory lies in the fact that, since the gametophytes derive their nourishment from food made by the sporophyte, they are independent of such external conditions as might interfere with the growth of a free-living gametophyte.

Except in the Anthocerotales, the sex organs of bryophytes are superficial structures, but in the pteridophytes they are embedded, either wholly or in part. Moreover, as compared with the sex organs of bryophytes, both the antheridia and archegonia of pteridophytes are reduced. The greatest reduction of spermatogenous tissue occurs in the heterosporous forms, reaching an extreme in *Isoetes*, where each antheridium produces only four sperms. The most primitive archegonia, those with the greatest number of neck canal cells, are found in *Lycopodium*. In nearly all the other homosporous pteridophytes there are either two neck canal cells or, more commonly, only one, this being usually binucleate. In the heterosporous forms there is a single neck canal cell that may be either binucleate or uninucleate, according to the genus. Nearly all pteridophytes have multiciliate sperms. Biciliate sperms, resembling those of bryophytes, are confined to *Lycopodium*, *Phylloglossum*, and *Selaginella*.

Interrelationships. The Psilophytales are the oldest known and most primitive group of vascular plants. Whether they were derived from ancestors resembling bryophytes or directly from alga-like forms is a matter of difference of opinion. It is rather generally agreed, however, that the Psilophytales gave rise to the other pteridophytes, since transitional forms have been found. The Lycopodiinae, Equisetinae, and Filicinae separated early from the Psilophytales and each has subsequently pursued an independent course of evolution. The Psilophytales also gave rise to the Psilotales, a group that has made relatively little progress and one that stands apart from the other existing groups.

The Lycopodiinae are a relatively primitive group in spite of the fact that some members have advanced to the condition of heterospory. They reached their climax in the Paleozoic and are now relatively unimportant members of the flora. There is no evidence that they have given rise to any of the higher groups. The Equisetinae, more advanced than the Lycopodiinae, also made their greatest display during the Paleozoic. They are a peculiar group with many features not seen in any other vascular plants. They also represent a line of evolution that ends blindly.

The Filicinae are the most highly developed of all pteridophytes and show much progress among themselves. It is generally believed, on the basis of much morphological and paleobotanical evidence, that the ferns have given rise to the seed plants. The leptosporangiate ferns are essentially modern, while the eusporangiate ferns are more ancient and more primitive. The Paleozoic ancestors of the spermatophytes must have developed heterospory, but the only known heterosporous ferns are the two families of Hydropteridales, both of which are modern and highly specialized. Yet, aside from heterospory, there are many resemblances between the eusporangiate ferns and the Cycadofilicales of the Paleozoic, which are the most primitive group of gymnosperms.

CHAPTER VIII

SPERMATOPHYTA

The spermatophytes constitute the highest and largest division of the plant kingdom, numbering approximately 196,000 species. They comprise the two classes Gymnospermae and Angiospermae, the former being not only the older and more primitive group, but by far the smaller one today. Spermatophytes are found in all parts of the world and in the most diverse habitats. Although the angiosperms dominate the land vegetation, they include members that have become aquatic, epiphytic, and, through partial or complete loss of chlorophyll, saprophytic or parasitic.

All spermatophytes are characterized by the production of seeds, a feature that at once distinguishes them from the lower groups. Like the pteridophytes, they are vascular plants with an independent sporophyte; but in spermatophytes the sporophyte attains its greatest complexity, while the gametophyte is obscure and so reduced that it is entirely dependent upon the sporophyte for its nutrition.

Spermatophytes range in size from the minute floating duckweeds, some no larger than the head of a pin, to the giant redwoods of California and certain eucalypts of Australia, both of which may reach a height of 100 m. All modern gymnosperms are woody plants, while the angiosperms include both woody and herbaceous types. The stem undergoes lateral branching, the branches nearly always arising in the leaf axils. Most commonly the branching is monopodial. Elongation of the root and stem is accomplished by a terminal meristem, never by an apical cell. All seed plants are heterosporous. The microsporangia and megasporangia are borne by members that are essentially foliar in nature but, although homologous with the sporophylls of pteridophytes, are nearly always more highly modified. Among spermatophytes it is customary to designate the microsporophyll as a *stamen*, the megasporophyll as a *carpel*, and the megasporangium as an *ovule*.[1] The megasporangium produces a single functional megaspore. Because the megaspore is not shed, the female gametophyte develops inside the megasporangium. This feature makes seed formation possible.

In practically all gymnosperms the female gametophyte produces archegonia, but in angiosperms archegonia are eliminated. The male

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[1] Really the megasporangium is only part of the ovule, *e.g.*, the nucellus.

gametophyte does not form antheridia, but gives rise directly to two sperms or their equivalent. Swimming sperms, universal throughout the bryophytes and pteridophytes, occur only in two orders of living gymnosperms, being replaced in all other spermatophytes by nonmotile male cells. In all seed plants the sperms or male cells, as the case may be, reach the egg through the agency of pollen tubes, within which they develop. Following fertilization, the embryo develops inside the ovule, which becomes a seed.

1. GYMNOSPERMAE

The gymnosperms, numbering only about 700 living species, are an ancient group with a long geologic history. All the evidence points to their origin from the ferns. They were abundant during the Paleozoic, while during the greater part of the Mesozoic they became the dominant group of land plants (Fig. 258). All existing gymnosperms are woody plants and most of them are trees. Gymnosperm means "naked seed," the seeds being borne not in a closed vessel, as they are in angiosperms,

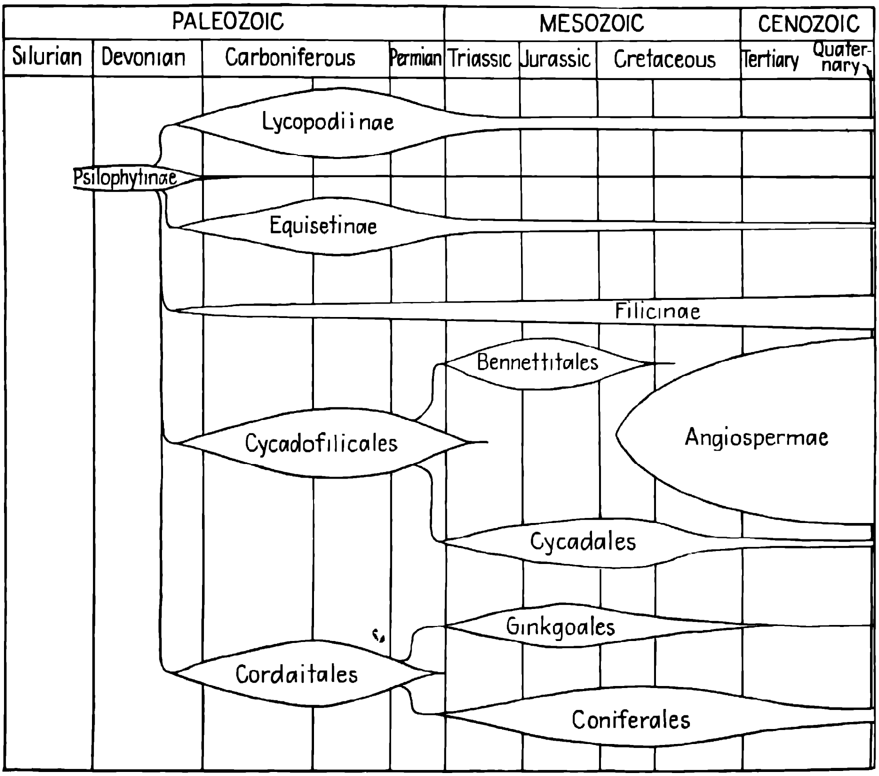

FIG. 258. Diagram showing the geologic distribution and the relationships of the major groups of vascular plants.

but freely exposed. The class includes seven orders: the Cycadofilicales, Bennettitales, Cycadales, Cordaitales, Ginkgoales, Coniferales, and Gnetales. Of these, the first, second, and fourth are entirely extinct.

1. Cycadofilicales

The Cycadofilicales[1] are the oldest and most primitive group of seed plants. Although some fossil remains have come from late Devonian deposits, the group did not become abundant and widespread until the Upper Carboniferous (Fig. 258). It declined greatly during the Permian, but persisted into the Triassic, when it soon became extinct. The Cycadofilicales are of great interest because, as their name implies, they are transitional between the ferns and the cycads.

Sporophyte. The general aspect of the Cycadofilicales was distinctly fern-like (Fig. 259). Some forms resembled modern tree ferns, but most of them were smaller. Some appear to have been climbers. The leaves, when found as impressions in the rocks, are so fern-like that they cannot be distinguished from the leaves of true ferns except when found in association with stems, sporangia, or seeds. The stem anatomy is fern-like also, but the development of secondary wood is characteristic. This wood consisted of pitted rather than scalariform tracheids. Three stelar types were represented among the Cycadofilicales, each constituting a "stem genus." *Heterangium* was a protostele, *Medullosa* a polystele (with three separate steles), and *Lyginopteris* an ectophloic siphonostele (Fig. 260). In each case the primary xylem was mesarch, a fern character. The leaf traces were double and direct; they were mesarch throughout.

Microsporangium. The microsporangia of the Cycadofilicales were at one time regarded as the sporangia of ferns. The microsporophyll (stamen) resembled an ordinary fern frond having fertile and sterile pinnae. In the "stamen genus" *Crossotheca* each fertile pinnule was more or less peltate and bore six to eight bilocular microsporangia on its lower side. This is designated as the "epaulet" type of stamen (Fig. 261*A*, *B*). Another, characteristic of the stamen genus *Calymmatotheca*, is known as the "cupule" type because the microsporangia were borne within a cup-like structure formed at the end of a naked branch (Fig. 261*C*). In some of the Cycadofilicales the microsporangia occurred as synangia on the abaxial surface of fern-like leaves.

Megasporangium. In none of the Cycadofilicales was a strobilus organized. Commonly the fern-like leaves were dimorphic, some being fertile and others sterile. The fertile leaves bore terminal ovules on their ultimate divisions (Figs. 196 and 259). The seeds were usually enclosed in a cupule (Fig. 262). As in other seed plants, the ovule consisted of a

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[1] Often called Pteridospermae.

FIG. 259. Portion of restoration of Carboniferous swamp forest in the Chicago Natural History Museum. Plants belonging to the Cycadofilicales include *Lyginopteris oldhamia*, a climber leaning against the large tree near the center, *Neuropteris decipiens*, in left center, and *Neuropteris heterophylla*, in lower left.

central portion, the *nucellus*, surrounded by an *integument* except at its apex, where a narrow passageway, the *micropyle*, was formed. In the Cycadofilicales the integument commonly was free from the nucellus only in the upper portion of the ovule, but in some cases was wholly free. The nucellus was prominently beaked and contained a deep pollen chamber in

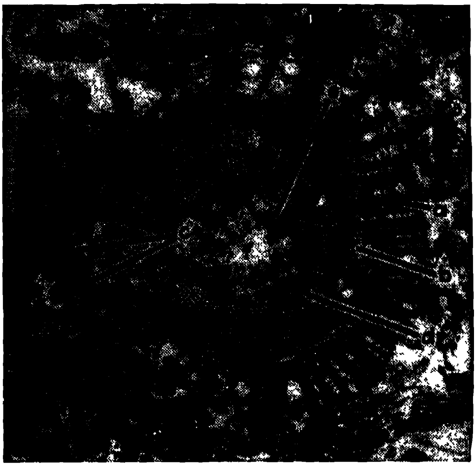

FIG. 260. Cross section of small stem of *Lyginopteris oldhamia*, ×5; *a*, sclerenchyma bands in outer cortex; *b*, inner cortex and phloem; *c*, double leaf trace; *d*, secondary xylem; *e*, primary xylem; *f*, pith. (*From Arnold.*)

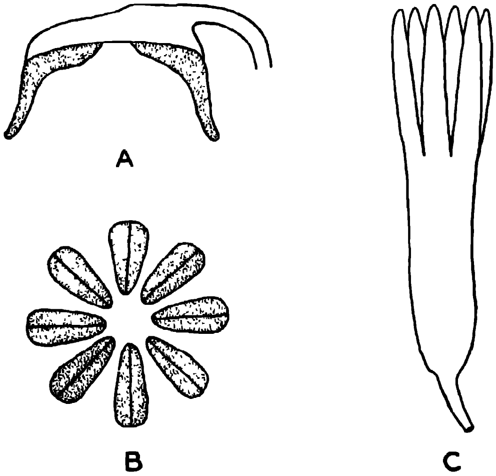

FIG. 261. Microsporangia of Cycadofilicales. *A*, diagrammatic longitudinal section of a fertile pinnule of *Crossotheca*, showing epaulet type with peltate limb and pendent sporangia, ×3; *B*, cross section of same, showing bilocular sporangia; *C*, cupule type, *Codonotheca*, with sporangia on the inner surface of the valves, natural size. (*A and B, after Kidston; C, after Sellards.*)

which the microspores accumulated. The Cycadofilicales must have had swimming sperms.

Gametophytes. Pollen grains, found in pollen chambers, contain a tissue of numerous cells, all of which were probably spermatogenous. The sperms seem to agree in form with those of existing cycads. No evidence of pollen tubes has ever been found and it is probable that they were not produced. Remains of the female gametophyte are fragmentary, but it is certain that archegonia were developed in the micropylar region of the nucellus, the microspores apparently coming directly in contact with them. No embryos have ever been found in the seeds, perhaps because they did not develop until after the seeds had been shed.

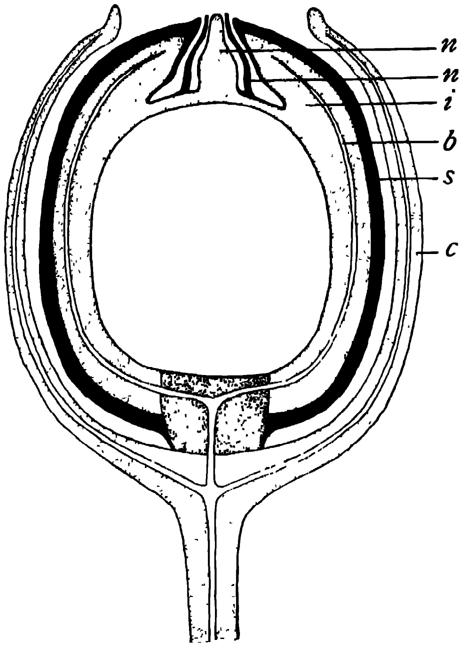

FIG. 262. Diagrammatic longitudinal section of the ovule of *Lyginopteris oldhamia* (*Lagenostoma lomaxii*) with its investing cupule; *n*, central portion of nucellus; *n'*, outer hardened portion with the pollen chamber between; *i*, inner fleshy layer of integument; *b*, vascular bundle; *s*, outer stony layer of integument; *c*, cupule. (*After Oliver.*)

Summary. The Cycadofilicales are a group that was dominant in the Paleozoic. It is closely related to the Filicinae, the general habit, leaves, and microsporangiate structures being distinctly fern-like. The vascular anatomy is also fern-like, but with the addition of secondary wood. Three stelar types are represented. A primitive feature is the occurrence of mesarch xylem throughout the plant, an advanced feature, the presence of pitted tracheids. There is no strobilus and the sporophylls are leaf-like and not highly differentiated from foliage leaves. The microsporangia resemble fern sporangia in being numerous on the sporophylls, but the megasporangia, in forming seeds, show a great advance. The Cycadofilicales are transitional between the ferns and cycads. They were probably ancestral to both the Bennettitales and Cycadales.

2. Bennettitales

The Bennettitales were a Mesozoic order, world-wide in distribution. They ranged from the Triassic to the Upper Cretaceous but reached their greatest display during the Jurassic (Fig. 258). The four principal genera are *Cycadeoidea*, *Williamsonia*, *Williamsoniella*, and *Wielandiella*. In spite of their many distinctive features, the Bennettitales were probably direct descendants of the Paleozoic Cycadofilicales.

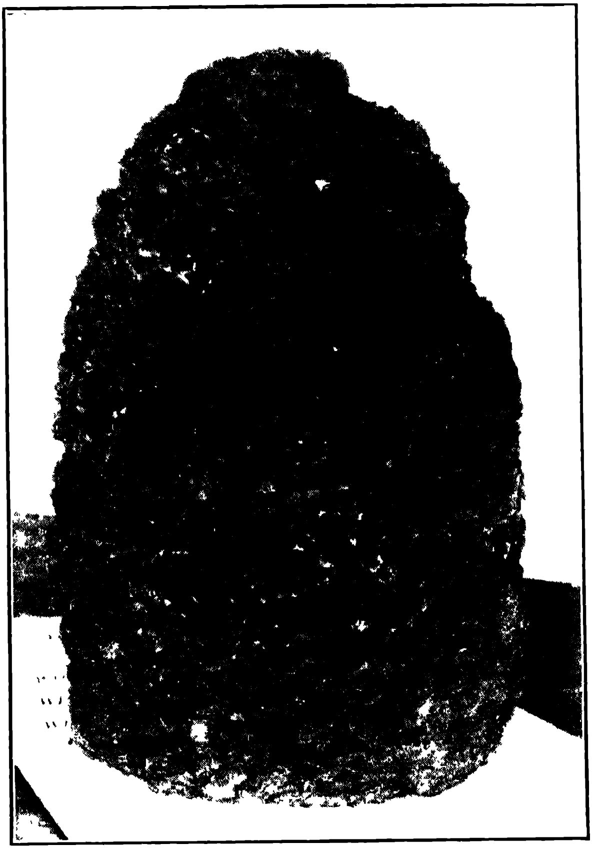

FIG. 263. Upper part of a large stem of *Cycadeoidea*. Some of the strobili are projecting and some have fallen out, leaving cavities. The specimen is about 60 cm. high.

Sporophyte. The Bennettitales were more diversified in habit than modern cycads. Few forms exceeded 2 m. in height and most of them were under 1 m. The stems of *Cycadeoidea* were mostly short, stout, and unbranched (Fig. 263), while those of *Williamsonia* were tall and columnar, often with a few lateral branches. They bore a crown of large fern-like leaves at the summit. The stems were covered with an armor of persistent leaf bases and a mass of woolly scales, forming a ramentum, as in many tree ferns. The stems of *Williamsoniella* and *Wielandiella* were slender, dichotomously branched, and smooth, with a cluster of leaves at the points of forking. Except in *Williamsoniella*, the leaves of the Bennettitales were pinnately divided into many leaflets.

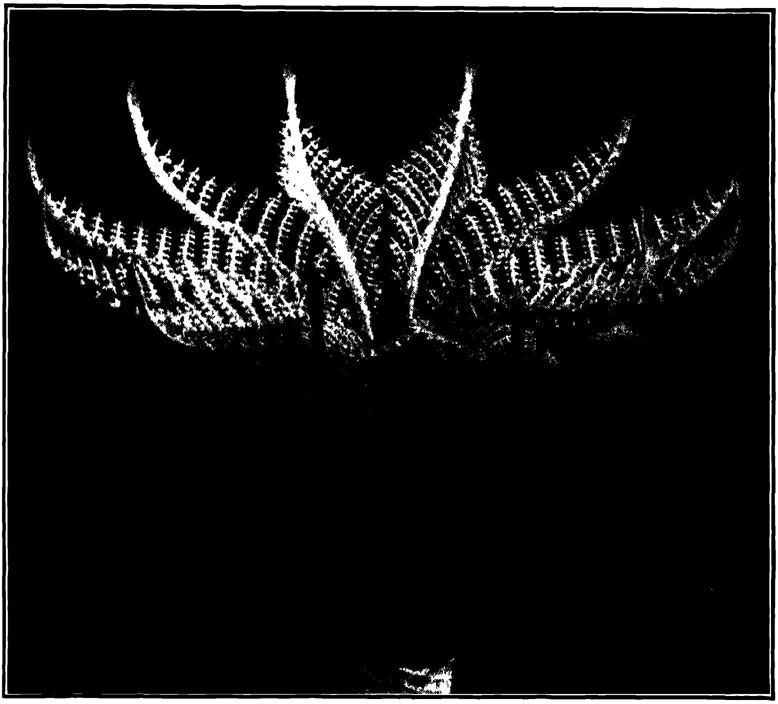

FIG. 264. *Cycadeoidea ingens.* Photograph of a model of the strobilus in the Chicago Natural History Museum.

The stem was an ectophloic siphonostele, a cross section showing a large pith, a thin vascular cylinder, and a thick cortex. The vascular bundles were collateral and endarch. Secondary wood, although scanty in amount, was always present. Most of the tracheids were scalariform, but in some cases were pitted. The leaf traces were single and direct, becoming mesarch after entering the leaves.

Strobilus. In *Cycadeoidea* numerous strobili were borne on short stalks occurring among the leaf bases, each strobilus being axillary (Fig. 263). In *Williamsonia* the cones were long-stalked and borne in the apical crown of leaves. In the two other genera the strobili were borne singly in an upright position where the stem underwent forking. The order is characterized by bisporangiate strobili (mostly monosporangiate in *William-*

sonia), the two kinds of sporophylls having the same relation to each other as have the stamens and carpels in a flower of the magnolia. Each cone consisted of four sets of members: an outer sheath of sterile bracts, a whorl of microsporophylls, stalked ovules, and interseminal scales (Fig. 264).

In *Cycadeoidea*, the microsporangiate structures had advanced but little beyond the fern condition. The microsporophylls (stamens), 10 to 20 in number, were large, leaf-like, and pinnately divided, each division bearing two lateral rows of abaxial sporangia borne in synangia like those of the Marattiales (Fig. 265). The megasporophylls and interseminal scales were closely crowded together at the summit of the strobilus axis, forming a compact ovoid body. Each ovule was borne at the end of a stalk that probably represents a reduced sporophyll (Fig. 266*A*). The stalks were more or less vertical, the middle one being the longest. The interseminal scales probably represent sterile sporophylls. The ovule had a basal cupule and a three-layered integument consisting of an outer fleshy, a middle stony, and an inner fleshy layer. The micropyle was

FIG. 265. Diagram of a longitudinal section of the strobilus of *Cycadeoidea*, showing hairy bracts below, two pinnate microsporophylls, and the central ovule-bearing axis. (*After Wieland.*)

long, and a prominent nucellar beak and pollen chamber were developed (Fig. 266*B*). Thus it seems certain that the Bennettitales had swimming sperms. Nothing is known of the gametophytes. The embryo was dicotyledonous and completely filled the seed, no endosperm having been present at maturity.

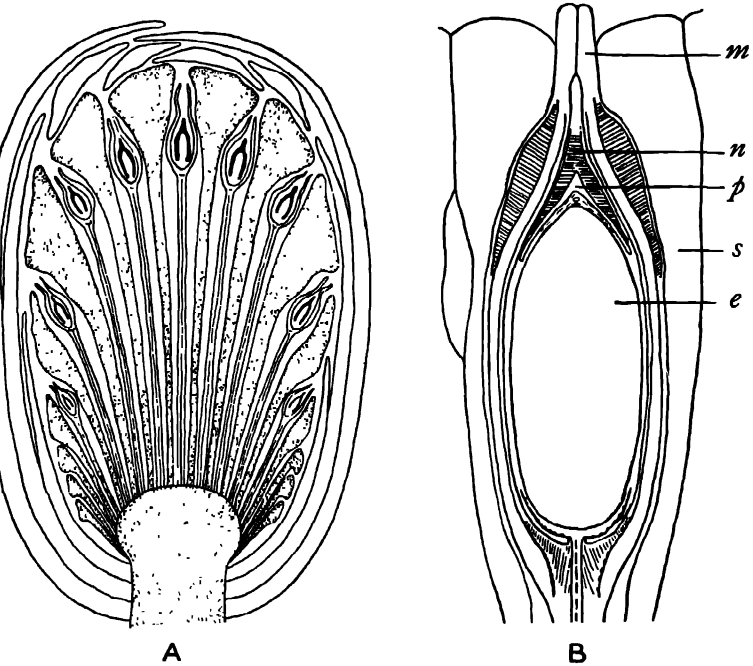

FIG. 266. Strobilus and seed of *Bennettites* (*Cycadeoidea*). *A*, diagram of seed-bearing strobilus, showing sheathing bracts, long-stalked seeds, and interseminal scales; *B*, longitudinal section of seed; *m*, micropylar tube; *n*, nucellar beak; *p*, pollen chamber; *s*, interseminal scale, *e*, embryo space. (*A*, *after Scott and others; B, after Wieland and Lignier.*)

Summary. The Bennettitales are a group dominant in the Mesozoic and intermediate in some respects between the Cycadofilicales and the Cycadales. Characters common to the Cycadofilicales include branching of the stem, a ramentum, direct leaf traces, leaf-like microsporophylls with synangia, and the ovule structure. An advance is seen in the organization of a strobilus. Characters common to the Cycadales are the general habit of some of the genera, the leaves, and the vascular anatomy, the stem being an endarch siphonostele with relatively little secondary wood. Distinctive features of the group are the bisporangiate strobili and the occurrence of both fertile and sterile megasporophylls, the latter bearing solitary terminal ovules. The Bennettitales are considered too specialized in their spore-bearing structures to have given rise to the Cycadales. Both groups seem to have had an independent origin from the Cycadofilicales. The resemblance between the bisporangiate cycadeoid cone and the flower of the magnolia and its allies has suggested that the angiosperms may have been derived from the Bennettitales, but there is little evidence to support this view (see page 411).

3. Cycadales

This order includes 9 living genera and about 100 species, all of which are tropical or subtropical in distribution. Four of the genera belong to the Western Hemisphere and five to the Eastern Hemisphere. *Zamia*, the largest genus, has about 30 species; it ranges from Florida to Chili. *Microcycas* is confined to western Cuba, *Dioon* and *Ceratozamia* to southern Mexico. *Cycas*, with 20 species, ranges from Japan to Australia and Madagascar. *Bowenia* and *Macrozamia* are found only in Australia, *Stangeria* and *Encephalartos* only in Africa. The Cycadales are closely related to the Bennettitales and like them were probably derived directly from the Cycadofilicales. They flourished throughout the Mesozoic and reached their greatest display in the Lower Cretaceous, when they were much more widespread than they are today (Fig. 258).

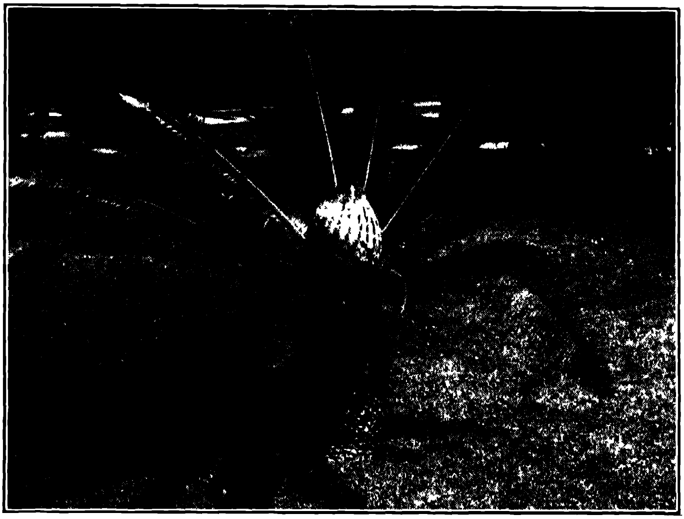

FIG. 267. *Dioon edule* with a large female cone 28 cm. in diameter. The leaves are up to 1.5 m. long.

Sporophyte. The stems of cycads are either subterranean and tuberous or aerial and columnar. They bear a crown of large fern-like leaves (Fig. 267). The stems of the columnar forms are covered with an armor of persistent leaf bases. The stem is rarely branched and is commonly less than 3 m. high. The tallest species (*Macrozamia hopei*) sometimes reaches a height of 18 m. The leaves are pinnate (bipinnate in *Bowenia*) and are borne in close spiral arrangement at the apex of the stem. They are rather tough and leathery and vary in length from 5 cm. to 3 m., depending on the species. The venation, often described as parallel, is really dichotomous, as in most ferns (Fig. 268*A*). In *Cycas*, however, the leaflets have no veins except a prominent midrib. The vernation is circinate in *Cycas* and either erect or somewhat circinate in the other genera (Fig. 268*B*).

FIG. 268. Leaves of cycads. *A*, two leaflets of *Zamia skinneri*, showing dichotomous venation, one-half natural size, *B*, young leaves of *Cycas circinalis*, showing circinate vernation, one-fifth natural size.

The stem of the Cycadales is like that of the Bennettitales in being an ectophloic siphonostele with a large pith, a thin vascular cylinder, and a thick cortex (Fig. 269). The vascular bundles of the stem are collateral and endarch, but the leaf traces, leaf veins, and bundles of the strobilus axis are mesarch and frequently amphicribral as well. Secondary wood is developed but is commonly small in amount. It consists of tracheids with bordered pits, except in *Zamia* and *Stangeria*, where the tracheids are scalariform, like those of ferns. The leaf traces of cycads are peculiar in being double and indirect. This means that, in passing from the stele